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THE JOURNAL
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Comparative Neurology

A QUARTERLY PERIODICAL DEVOTED TO THE
Comparative Study of the Nervous System.

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THE
JOURNAL OF COMPARATIVE NEUROLOGY.

VOLUME X—NUMBER I.

THE SENSE-ORGANS OF NEREIS VIRENS, SARS.¹

By FANNY E. LANGDON.

With Plates I to III.

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¹ Work from the Zoölogical Laboratory of the University of Michigan, Jacob Reighard, director.

I. INTRODUCTION.

The following work¹ was begun in the Zoölogical Laboratory of the University of Michigan in 1894 under the direction of Prof. Jacob Reighard and has since been carried on there except during the summer of 1896. At this time, the application of the intra-vitam methylene blue stain to the material in hand was worked out in the Marine Biological Laboratory at Woods Hole under the direction of Prof. A. D. Morrill of Hamilton College.

With the exception of the four eyes, none of the sense-organs of *Nereis virens* have previously been described, though paired cephalic sense-organs of unknown function and isolated epidermal sensory cells have been described in other species of this genus and the latter have been briefly mentioned for *N. virens* itself. The following account contains a detailed description of two kinds of sense-organs—*diffuse sense-organs* and *spiral organs*—which are found scattered over the body in the epidermis of this worm, and also a brief description of two pairs of organs which are found in the prostomium. The diffuse sense-organs are simple epidermal organs which are directly comparable with the epidermal tactile organs of the Oligochæta. Isolated sensory cells, which are similar to the cells of the organs described in this paper and may prove to be identical with them, have been described for other species of *Nereis*; the diffuse sense-organs themselves have never been described for *Nereis* but have recently been described for two other genera of the Polychæta—*Axiothea* and *Clymene*. The spiral organs are complicated organs whose structure differs considerably from that of any organ previously described. They are, however, so nearly like the epidermal ocular organs of various invertebrates, that they may be considered to have for their function the perception of light. The two pairs of cephalic organs are of problematical function and have been already found in other Polychæta.

¹ A brief abstract appeared in *Science*, Vol. V, p. 427 (1897).

A peculiar form of epidermal cell has been incidentally noted. This cell apparently serves as an anchoring cell for the peripheral ends of muscles.

II. METHODS.

My material was obtained along the southeastern coast of New England; it was used in part at once and in part after shipment to Ann Arbor. It was found that the worms which were simply left in the open jar of sand and sea weed in which they had been shipped kept better than those which were placed in artificial sea water. The sand and sea-weed were kept loosely packed and the water lost by evaporation was replaced by distilled water.

Alcohol used as a killing fluid rendered the cuticula so resistant as to interfere with sectioning, but Müller's fluid without the use of anaesthetics gave very good results. When this fluid was used, the cuticula did not become resistant, the tissues stained readily afterward, and the epidermal structures were very well preserved. Paraffin sections were cut $10\ \mu$ thick and mounted by Pringle's variation of the hot water method as given by Lee. I find if my slide is chemically clean, the sections perfectly straightened, and then allowed to dry fully 24 hours before further manipulation, there is not the slightest need of any fixative with this process. The slides may be carried through a complicated process afterward without losing a section. Kleinenberg's hæmatoxylin gave the best results for general work and for a study of the spiral organs. The Biondi-Ehrlich three color mixture, lithum carmine followed by Lyons blue, and Licht-grün followed by orange G were useful for differentiating glandular tissues.

For special nerve stains, both the silver nitrate and the methylene blue were tried; the silver nitrate proved so difficult and the methylene blue so easy that finally the latter was used exclusively. The method used was in general that given by Bethe ('95). It was found absolutely necessary that the circulation of the worm should be vigorous at the time of injection; in this case the blood-vessels would be filled with the blue and the nerve tissues well stained; but if the circulation were feeble at the time of injection, the blood-vessels would be found to be filled with clotted blood and but little if any of the nerve-tissue would be stained.

My best results were obtained as follows: Vigorous worms were injected with $1\frac{1}{2}\%$ Ehrlich's methylene blue in normal salt solution. The injection was made into the body cavity of the worm, care being taken not to inject enough in any one place to cause much swelling. The

blue could be seen to pass from the metamere injected through several adjacent metameres. When the body wall began to be distended, an injection was made in another region and this was repeated until the entire body cavity seemed to contain the blue. At first the attempt was made to force in as much fluid as possible at one injection, but this injured the tissues so that it seriously interfered with the circulation. Then injecting a smaller amount and repeating the injection after a short interval was tried—a method also used by Meyer ('96); this always gave very satisfactory results. Usually each worm was injected three times at intervals of about 40 min., using each time great care not to injure the animal more than was absolutely necessary. After the first injection, much more of the stain could be forced in at a time without danger of rupturing the body wall.

Following a suggestion given me by Dr. G. C. Huber, the animals were put away in the dark after each injection. It was found that, if two worms of equal size and apparent vigor were injected with equal amounts of the same methylene blue solution, the one kept in the dark gave surprisingly richer results than the one kept in the light. Instead of leaving the injected worm directly exposed to the air, it was found better to keep it in its normal medium—the sea-water. About four hours after the first injection—a shorter time on very warm days—the worms were taken out and, without being opened, exposed to the light and air. At first the color of the body would be nearly normal, but in about fifteen minutes it would become a rich blue. I am, however, inclined to believe that this exposure causes merely a bluing of the general tissues and that the nerve elements are already stained when the animal is removed from the dark and the sea-water. Several times a worm was removed from the dark and while it was still in the sea-water, a parapodial cirrus was cut off. No matter how quickly this was placed under the microscope, the nerve-cells of the sense-organs were already blue. Sometimes a worm would be so laid that only the parapodia of one side would be directly exposed to the air, yet the nerve tissues of the parapodia from the opposite side would be as richly stained as those from the exposed side. Then, again, several times the brain was richly stained in worms that had not been opened in this region. These facts seem to indicate that direct exposure of the nerve tissues themselves to the air is not always necessary.

My own observations have led me to the conclusion that the main factors in obtaining a rich stain in *Nereis* are: 1. vigorous, healthy worms; 2. the injection of a large quantity of strong stain in such a manner as to avoid interfering with the circulation; and 3. the keeping

of the animals under as nearly as possible normal conditions for a time long enough to allow the stain to be carried all over the body by the blood-vessels.

The same worm can be used for study for from three to five hours after removal from the dark, probably even longer. When a part of the body was mounted in sea-water and covered with a cover-glass, the stain quickly faded from all parts except the nerve-elements, which kept the stain from one half to three quarters of an hour.

Parts of the worm which were to be preserved were dropped into Bethe's fixing fluid (invertebrate formula) which had been previously cooled. The tissues were kept on ice in this fluid for from 4 to 6 hours—or even over night if convenient. They were then washed in a large quantity of distilled water for from 10 to 12 hours, and passed quickly, but by gradual steps, through the various grades of alcohol. The specimens were not only kept on ice, but each grade of alcohol was cooled before using. It was not only found that the warm alcohol removes the stain, as stated by Bethe, but also that warm water does the same. Several times tissues which a microscopical examination showed to be richly stained up to the time of warming for the paraffin bath, were at once ruined by this process and permanent mounts of such tissues showed that they had not been thoroughly dehydrated.

Pure xylol proved to be the best clearing fluid; the transfer from the absolute alcohol to the xylol was made gradually and the xylol kept on ice until all trace of the alcohol was removed. The tissues were warmed gradually to the melting point of the paraffin used and kept for two or three hours in the paraffin which was changed once or twice before embedding. When embedded in paraffin, even if the paraffin is allowed to cool before all the xylol is removed, the tissues retain the stain well. Material which had been kept in a block of soft paraffin for six months before cutting was in excellent condition and was uninjured by re-embedding.

The sections were cut from from 20 to 45 μ thick, and fixed to the slide by means of albumen fixative—the warm water method proving unsatisfactory in this case since it seemed to injure the stain. Mayer's alcoholic cochineal, which stains in 10 min., proved to be the best secondary stain. While in the grades of alcohol and in the stain itself the sections were kept cold; they were cleared in xylol and mounted in xylol balsam. Sections thus prepared show no sign of losing their blue after an interval of three years. The only epidermal structures not well preserved in these preparations are the spiral organs. Lewis ('98) states that the cuticula in *Axiotea* and *Clymene* is badly pre-

served in methylene blue preparations; in *Nereis* I have always found it very well preserved and its structure, especially after the use of the secondary stain, clearly defined.

The removal of the cuticula of *Nereis virens*, owing partly to its greater thickness and partly to the fact that it is more firmly attached to interior structures, is much more difficult than in *Lumbricus*. The alcoholic method used with the latter form (Langdon '95) was a total failure when tried on *Nereis*. Macerating in Müller's fluid for three months gave better results, but my best results were obtained with a 10% salt solution, suggested to me by Miss Margaret Lewis (see Lewis, '98). I found it best to prepare the cuticula as follows: The worms were killed in the 10% salt solution and left for a few days in a small quantity of this fluid. They were then washed thoroughly in plenty of distilled water to remove all trace of the salt, and placed in 35% alcohol to render the cuticula firmer. Each worm was then slit its entire length close to the parapodia of one side, all the parapodia of the other side were cut off, and the body wall cut through along the anterior margin of the buccal cavity. The greater part of the interior tissues were removed with fine forceps and the inside of the cuticula brushed clean. It was found difficult to get all the tissues out of the cephalic cirri. All could be removed from the palps and tentacles and some from the cirri by turning the structures inside out with a pipette, brushing the inner surface, and then turning them back again by the action of the pipette on the opposite surface. When it was desired to mount the cuticula of a given parapodium, the latter, while still attached to the body cuticula, was turned wrong side out, cleaned, turned back again, and then cut off and mounted separately. After being thoroughly rinsed in clean 35% alcohol, the cuticula was cut into convenient lengths, floated onto a slide, pressed down with a brush, and then allowed to dry. The cuticula of the caudal region macerates so quickly that it is best to cut off this region and mount its cuticula after it has been in the salt solution a shorter time than that allowed for the rest of the body.

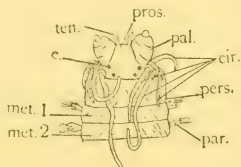
For making a chart to show the distribution of the sense-organs by means of the cuticula, a Zeiss projection microscope fitted with an arc-light was used; it was found that the image of the cuticula was more distinct when the room was not darkened. The distribution of the organs in the various sensory appendages was also studied by means of surface views of living appendages taken from worms that had been injected with the methylene blue. In such appendages the

cuticular location of each sense-organ is shown by a clear white spot in the surrounding blue stained tissue.

Owing to their minuteness, the external openings of the spiral organs could not be distinguished in the removed cuticula. The distribution of these organs in the head and first metamere was studied by means of a wax model of this region. In making this model it was necessary, owing to lack of material, to make use of a series of sections only 10 μ thick and prepared for another purpose so that there were no reference planes; but there are so many grooves and ridges on the surface of the anterior end of *Nereis* that it was easy, by their aid, to fit the sections together accurately. As each organ appears in at least two sections, only every other section was drawn and the position of each organ was marked in its margin. After the sections were cut out and as they were being fitted together, common pins were stuck into the model so that their heads marked the position of the outer ends of the spiral organs on the surface of the model.

III. EXTERNAL APPEARANCE OF NEREIS VIRENS.

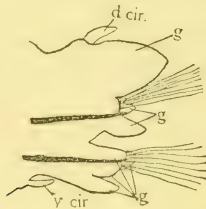
The following brief description is inserted for the convenience of the reader. The body of *Nereis virens* is in general cylindrical, and beside the head itself consists of about 120 metameres. The head consists of a prostomium joined to the dorsal border of the anterior margin of a wide peristome which is supposed to consist of two fused metameres (see Text-figure 1). The prostomium bears the four eyes



Text-figure 1. Outline of the dorsal surface of the cephalic end of *Nereis virens*. *cir.*, cephalic cirrus; *e.*, eye; *met.*, metamere; *pal.*, palp; *par.*, parapodium; *per.*, peristome; *pros.*, prostomium; *ten.*, tentacle.

on its dorsal surface, a pair of palps on its lateral border, and a pair of tentacles on its anterior border. Each tentacle is a small appendage which tapers to a point. Each palp consists of two parts—a thick basal part and a smaller rounded tip which can be almost wholly retracted into the basal part; the body cavity extends into the basal part but not into the tip. Just caudad of the base of each palp, the peristome bears

two pairs, set very close together, of long slender appendages—the cephalic cirri. One cirrus of each pair is over twice as long as the other one. Each cirrus is inserted on a short basal part similar to but smaller than the basal part of a palp, and is kept constantly moving in all directions. The surface of the peristome and of a few of the anterior metameres is marked by numerous grooves which pass obliquely from their anterior to their posterior borders. Each metamere back of the peristome bears on each lateral surface a parapodium—a lobed outgrowth of the body wall (see Text-figure 2). A typical parapodium consists of about seven comparatively flat, pointed lobes which func-



Text-figure 2. Outline of a typical parapodium of *Nereis virens*. *d. cir.*, dorsal cirrus; *g.*, gill lobe; *v. cir.*, ventral cirrus.

tion as gills and of two slender pointed appendages—the dorsal and ventral parapodial cirri—which are purely tactile. The anterior parapodia are very small; passing caudally they increase in size until near the caudal end of the worm. At this extremity, the metameres become very small; the parapodia also decrease in size but are much larger in comparison with the size of the metameres than are the parapodia of the cephalic end of the worm. The anal metamere bears a pair of long slender appendages similar to the cephalic cirri and known as the anal cirri. These cirri are directed backwards.

IV. THE DIFFUSE SENSE ORGANS.

The diffuse sense-organs are found not only in the epidermis over the entire body but also in each of the cephalic and anal appendages and in each lobe of every parapodium. Each organ consists of a small elongated group of bipolar nerve-cells whose central ends taper into nerve fibers which pass into the central nervous system, and whose peripheral ends also taper into processes which pass through modified areas in the cuticula

above each organ and project above the external surface as a group of sensory hairs. These sense-organs are directly comparable with the epidermal sense-organ of *Lumbricus* (Hesse '95 and Langdon '95) and of *Axiotea* and *Clymene* (Lewis '98). The sense-organs found in different regions of the body vary in the position of their cells, in the final termination of their peripheral processes, and in the character of the cuticular openings by means of which these processes reach the exterior. The organs of these various regions will, therefore, be described separately. Since those found in the epidermis of the body itself may be conveniently taken as a type, they will be first considered.

A. Structure.

a. *Diffuse sense-organs of the body epidermis.*—Each diffuse sense-organ of the body epidermis, as seen in the prostomium, peristome and first metamere, consists of from 5 to 8, rarely as many as 16, bipolar nerve-cells. These cells are arranged in a slender spindle-shaped group varying from 4 to 10 μ in width and from 16 to 20 μ in length (Plate II, Figs. 30-32) and *all of the cells in each group are situated entirely within the epidermis itself*. Each of these bipolar nerve-cells may be conveniently analyzed into three parts—the body of the cell, an enlarged part in which the nucleus lies, the central process or axis cylinder, a slender fiber-like part which arises from the central end of the cell-body, and the peripheral process, an equally slender part which arises from the peripheral end of the cell-body. The tip of this peripheral process is differentiated into a sensory hair which is raised above the external surface of the worm (Plate I, Fig. 9; Plate II, Fig. 34).

The body of an individual cell is about 4 μ wide and from 4 to 10 μ long, scarcely larger than its nucleus. The shorter cell-bodies round off abruptly at each end; the longer ones taper at one or both ends. From the central end of each cell, one and only one process arises. I have never found any division of this process nor any branches arising from it, but the cases in which I have been able to trace a central process until it

reaches a nerve are so few that I would not, perhaps, be justified in deciding that such a process never branches. Each central process is slightly sinuous in its course; it takes such stains as Kleinenberg's hamatoxylin but lightly, appears finely granular, and is of uniform diameter. With the methylene blue method it becomes delicately beaded or coarsely varicose. In fact, it presents all the characteristic appearances of a nerve-fiber. All the central processes, or axis cylinders, which come from the same group of nerve-cells—i. e., from a single sense-organ—pass together in a slender bundle between the central ends of the epidermal cells to the base of the epidermis.

In the base of the epidermis, as is easily seen in sections, are many nerve bundles which can be traced directly into the central nervous system. Even when a cell in one of the diffuse sense-organs is stained intensely blue, it usually happens, in my preparations, that the central process itself is stained for only a short distance centrally from its cell. Moreover, the entire bundle of nerve-fibers from one sense-organ is not only very slender, but always passes to the base of the epidermis in a more or less undulating course so that it is often cut obliquely. These facts render it usually impossible to trace either a single peripheral process or the entire bundle itself into one of the epidermal nerves. In two cases, however, the bundle of central nerve-fibers from an organ turned obliquely in the plane of the section and entered a cross section of an epidermal nerve (Plate II, Fig. 30). Moreover a central process itself in each of these bundles was stained blue for a longer distance than usual and could, therefore, be traced continuously. These two cases may be taken as evidence, it seems to me, that the central processes from all the diffuse sense-organs enter the nerves lying in the base of the epidermis. As will be seen later, this conclusion is abundantly supported by a study of the diffuse sense-organs of the various tactile appendages. In these it is clearly seen that all the central processes pass directly into nerves which in turn pass directly into the central nervous system.

The peripheral end of each cell gives rise also to but a single process. The latter passes, in company with the other

peripheral processes of the cells of the same organ, to the base of the cuticula covering the organ in question. Each peripheral process presents exactly the appearance of a central one. Therefore, as far as morphological appearances go, it is necessary to consider each peripheral process as well as each central one a true nerve-fiber; as will be seen later, a functional interpretation tends to confirm this opinion. When the peripheral processes from an organ reach the cuticula, they enter, still in a bundle, the differentiated area which always exists in the cuticula immediately over each sense-organ.

The cuticula over the body of *Nereis virens* is composed of a thin outer and a very thick inner layer (Plate II, Figs. 30 and 34). The outer layer is only $2\ \mu$ thick and, as seen in sections, is clearly marked by straight striations perpendicular to its outer surface. These striations mark the lines of separation between the individual fibers of which this layer is composed. The inner layer is $18\ \mu$ thick and is faintly marked by undulating striations parallel to the outer surface. In such stains as Kleinenberg's hæmatoxylin and Biondi-Ehrlich, the outer layer takes a much deeper stain than the inner so that the plane separating the two can be clearly seen. Bayer ('98) has found in the Rhynchobdellidæ that the cuticula is composed of layers of different ages, that the striations in the cuticula which run parallel to its outer surface represent the planes of separation between these layers, and that the outermost layer is frequently shed. I know of no observations on the shedding of the cuticula in the lower Annelids but the wear to which the cuticula is subjected by external forces, the strain to which it is subjected by the growth and movement of the worm itself, and also the fact that the outermost layer is so easily detached from the rest of the cuticula in both *Nereis* and *Lumbricus* render it probable, it seems to me, that in the lower Annelids the outer layer of the cuticula is either occasionally shed or gradually worn away. Then the undulating striations in the thick inner layer of the cuticula of *Nereis* would represent planes separating the successive layers. The breaking up of the outermost layer into fibers may be due to the weakening of this layer with age.

The above mentioned differentiated area in the cuticula over each sense-organ consists of two cavities—a larger ovoid cavity in the inner layer of the cuticula and a shallow cavity in the outer layer—separated by a thin layer which is perforated by several fine canals (Plate II, Fig. 34; Plate I, Fig. 9). Each of these ovid cavities is 16 or $17\ \mu$ deep. A cross section of it taken at any part of its height always presents a circular outline. A longitudinal section shows that the smaller end of the cavity is next to the epidermis and is about $4\ \mu$ in

diameter; the diameter increases gradually until, at the peripheral end of the cavity, it becomes about $8\ \mu$. This ovoid cavity does not extend entirely through the inner layer of the cuticula, but is bounded peripherally by a thin layer of the latter—a layer which forms the perforated membrane previously mentioned. The membrane is about $2\ \mu$ thick, is slightly concave on both sides, and is pierced by from 5 to 16 minute canals. Over it is the cavity in the outer thinner layer of the cuticula. This cavity is really an opening which apparently extends entirely through the outer layer of the cuticula. This opening, together with the slight concavity in the outer side of the perforated membrane itself, forms on the outer surface of the cuticula over each sense-organ a saucer shaped depression slightly more than $2\ \mu$ in depth and about 6 or $8\ \mu$ in diameter (Plate I, Fig. 11).

The entire bundle of peripheral processes from a single sense-organ enters the ovoid cavity of its own differentiated area and passes through this cavity to the perforated membrane. Here the peripheral processes terminate in sensory hairs which pass through the canals in this membrane into the outer cuticular cavity and in the latter form a brush-like group which projects stiffly above the external surface of the body. Usually each peripheral process bears a single sensory hair which passes directly through one of the canals in the perforated membrane to the exterior. In a number of cases, however, I could distinctly see that before passing to the exterior a peripheral process branched into at least two or three processes (Plate II, Fig. 37), thus bearing several sensory hairs, each of which passed through a canal of its own. Owing to the difficulty of obtaining a side view of a cluster of sensory hairs in the removed epidermis, I found it impossible to study those of the general epidermis in the living condition. In material killed by alcohol or Müller's fluid and stained by the usual stains, not only are the cuticular canals but dimly seen, but the sensory hairs are usually withdrawn so that their tips lie either within the canals of the perforated membrane or even beneath the latter in the ovoid cavity itself. I am, therefore, unable to state how far

above the surface these sensory hairs normally project, but, from what I have seen, I am inclined to think it is not very far (Plate I, Fig. 9).

The fact that the perforated membrane is found only in the outer part of the thick inner cuticula and the only cells going to it are the bipolar nerve cells would at first seem to indicate that it is formed once for all. If, however, the outer surface of the cuticula of *Nereis* is either shed or worn away, there must be some provision for the regeneration of the perforated membrane. It may be that the epidermal supporting cells, acting through the thick cuticula, control the formation of a new perforated membrane, or it may be that the nerve cells themselves possess the power of forming cuticula. The latter explanation seems to me the more probable one. Then the extreme thinness of the perforated membrane as compared with the thickness of the general cuticula could be accounted for by supposing that the nerve cells, being highly specialized for another purpose, had retained the power of secretion in but a slight degree. The above supposition must, of course stand or fall by a study of the embryological development and of normal regeneration. Any difficulty in meeting the problems involved cannot, however, be taken as a proof that in *Nereis* or any other worm, the cuticula is an unchangeable formation because in the *Rhynchobdellidæ*, which are known to shed the outer layer of the cuticula, there are epidermal sense-organs above each of which is a perforated membrane.

In the methylene blue preparations, the processes in the cuticular cavities are often variously distorted (Plate II, Figs. 30, 34 and 37). Sometimes a fiber is abnormally thick and ends just under the perforated membrane in a small knob from which one, two, or three finer processes—the sensory hairs—pass through the canals of this membrane. The sensory hair may be normal while somewhere in the course of the peripheral process through the inner cuticular cavity there may be one or more varicosities of various sizes, or the peripheral process may appear normal while the sensory hair itself is swollen into a ball which lies above the cuticula. When these varicosities exist in the peripheral processes themselves, the withdrawal of the sensory hairs, as will be seen later, is due to their formation. In other cases it is due to a decided bending of that part of a peripheral process lying in the cuticular cavity, caused, perhaps, by the protoplasm of the fiber expanding or contracting more on one side than on the other.

In the methylene blue preparations that have been re-stained by the cochineal, there are often seen in each organ a

few cells and peripheral processes which were untouched by the blue but are now stained a deep pink by the cochineal (Plate II, Fig. 32). In these cases it can not only be seen that the bodies of these cells, like those stained by the blue, lie entirely within the epidermis; but that, in the body epidermis, *all the bodies of the cells of a sense-organ generally lie above the middle height of the epidermis*. I have seen but very few of these sense-organs whose cell-bodies reached almost to the base of the epidermis. The cells stained by the blue sometimes lie in the center, sometimes in one or both margins of an organ; the cells stained pink are not only exactly like the others but clearly send peripheral processes into the cuticular cavity over each sense-organ: it would therefore appear that *each diffuse sense-organ is composed of but one kind of cell and that cell is clearly a bipolar nerve-cell*. The epidermal cells around an organ show no signs of being modified into covering cells.

In forty organs especially examined for this point in sections of the peristome, only three showed but a single blue cell. Such cases might at first sight be taken as proof of the existence of isolated sensory cells, but in each of these three cases around the single blue cell there were found, by the use of the secondary stain, other cells which presented the same characteristic appearances as the blue cell. Moreover, whenever the cuticular cavity belonging to the organ in question appeared in the same section, there were found in this cavity not only the blue stained process of the blue cell, but also other peripheral processes untouched by the blue. These processes were entirely free from pigment, which is always found in the peripheral ends of the supporting cells of the epidermis—therefore they cannot belong to the common cells of the epidermis. In hundreds of diffuse sense-organs examined for various purposes, I have always found more than one cell. I therefore consider that I am justified in deciding that in the body epidermis of *Nereis virens* *there are no isolated sensory cells, the bipolar nerve cells there present are all grouped into definite sense-organs*.

b. Diffuse sense-organs of the appendages. In the thickened bases of the palps, of the cephalic cirri, and of the parapodia, the diffuse sense-organs are exactly like those found in the body-wall and the cell-bodies of these organs always lie in the epidermis itself.

In the slender distal portions of the cephalic and anal cirri, in the tips of the palps and in the tentacles and parapodial cirri, the diffuse sense-organs differ from those of the body itself mainly in the following points: the inner cuticular cavity, owing to the greater thinness of the inner cuticular layer in these appendages, is almost lacking, and the outer cavity is replaced by an elevation; the bodies of the cells of the sense-organs lie farther beneath the cuticula and those belonging to several sense-organs are often massed together so that a given group usually contains cells belonging to two or more organs.

Each of the appendages mentioned in the last paragraph is covered by a cuticula consisting of the same two layers found in the body cuticula, but in this region the inner layer is only 2 or 3 μ thick and the outer layer only 1 or 2 μ . Under the cuticula is a layer which is lacking in gland cells and is thus composed of but one kind of cell—the epidermal supporting cell. The bodies of these cells are 16 μ in length; they have their greatest width next to the cuticula and taper gradually to a pointed base which in every case is prolonged into one or more basal processes. These processes pass into the interior of the appendage and there, together with the processes from a few stellate cells which lie in this region, are loosely interwoven into fibrous tissue which fills the greater part of the appendages. In the longitudinal axis of each appendage, from its base almost to its apex, passes an axial nerve.

Retzius ('92a and '92b) has considered that in such appendages, the bodies of the epidermal cells form the epidermis itself, that the space between these bodies and the axial nerve—that is, the space filled by the basal processes of the epidermal cells—is beneath the epidermis; and that, therefore, the sensory cells which lie in this region have sunken beneath the epidermis. Pruvot and Racovitza ('95) and Racovitza ('96) have stated that in the Polychæta the "stylodes," i. e., the distal portions of the various sensory appendages—are purely epidermal outgrowths. In my work on *Nereis* I have myself been led to the same conclusion. In *Nereis* these appendages never contain an extension of the body cavity. In them are found only structures which are found in the epidermis of the body. In the latter, the bodies of the supporting cells of the epidermis are the same in form and almost the same in size as those of the appendages, but one never thinks of locating the base of the epidermis of the body at the base of the bodies of these cells. In this epidermis, the slender basal processes of the epidermal supporting cells are almost as long as the basal processes of similar cells in the appendages and extend centrally for a long dis-

tance before forming a basement membrane. This basement membrane lies between the epidermis itself and the layer of circular muscles just beneath it. In the distal parts of the cephalic, anal, and parapodal cirri, and in the tentacles there are no muscles whatever; those found in the retractile tips of the palps do not form a circular muscle layer, but are the ends of muscles which enter these appendages exactly as similar muscles enter the epidermis of the body itself. *These appendages must be, therefore, purely epidermal outgrowths—strictly homologous with the epidermis itself—and the base of the epidermis of any one of these structures can only be found at the base of the structure itself.* The axial nerves of each appendage would then be but one of the nerves which lie in the base of the epidermis and receives the central processes of several sense-organs.

It will be observed that the gills and the thickened bases of the palps and of the anal and cephalic cirri are not included in this discussion. All of these structures contain an extension of the body cavity and the base of the epidermis of each is, at least in places, limited by a basement membrane which lies in the structure itself and not at its base. These structures are, therefore, evaginations of the entire body wall and cannot be considered as differentiations of the epidermis alone.

It follows from the above that everything contained within the cuticula of the distal portion of the cephalic and anal cirri, in the retractile tips of the palps, and in the tentacles and parapodial cirri is in the epidermis; therefore *all the sensory cells in these appendages, no matter how far they lie beneath the cuticula, are really situated in the epidermis itself*, beneath the bodies of the epidermal cells, it is true, but among their basal processes.

In the cephalic cirri, the bodies of the cells of the diffuse sense-organs lie anywhere between the bodies of the epidermal cells and the axial nerve of the cirrus, but usually somewhat nearer the former. In these appendages I have seen nothing which can be interpreted as a sensory system of isolated nerve-cells—*all of the sensory-cells lie in definite groups* (Plate I, Fig. 1, Plate II, Fig. 33). The cells of any one group do not, however, always belong to a *single* sense-organ as is the case in the epidermis of the body. Sometimes all the peripheral processes from one group of sense-cells pass to a single modified area in the cuticula and in such a case this group constitutes a single sense-organ. Often the bundle of peripheral processes from a single group of sense-cells, before reaching the bodies of the epidermal cells, divides into two or three smaller bundles each of which passes to a separate area in the cuticula (Plate I, Fig.

2, and Plate II, Fig. 38). Such a group may be considered as made up of as many organs as there are cuticular areas to which its peripheral processes pass. In this case it may at first seem difficult to distinguish a grouping of cells into definite organs. But one may suppose that originally the sense-organs lay nearer the cuticula—as is the case in the body wall, that in the base of the epidermis the central fibers from several organs passed into a small nerve, and that several of these smaller nerves joined to form a larger one. If now the bodies of the cells of these organs sink centrally from their original position, their course would naturally be along the course of their central processes and they would come to lie somewhere in the original course of these processes. In those cases in which the central processes from two or more organs soon joined to form a common nerve, the bodies of the cells of these organs would come to lie side by side at this point of junction or even along the former course of this common nerve itself; and the original course of the outer portion of the central processes from these organs would be shown by the final position of the inner portions of their peripheral processes. *In the cephalic cirri, therefore, I consider that one of the modified areas through which a group of sensory hairs pass to the exterior, the small bundle of peripheral processes going to this area and bearing these sensory hairs, and the cells giving origin to these peripheral processes, whether associated with cells belonging to other organs or not, constitute a sense-organ.* Such an organ would be directly comparable with the diffuse sense-organs found over the general body of *Nereis*.

In these cephalic cirri, a group of sensory cells varies in length from 25 to 80 μ , in width from 12 to 16 μ , and contains from 7 to 16 cells. The cells composing a single group lie at different depths beneath the cuticula (Plate I, Fig. 1). Occasionally the body of one cell is separated from the others, but usually the body of one fits between the tapering ends of others. There is a greater difference in the form of these cells than is found in the cells of the diffuse sense-organs of the body epidermis, seemingly because in the latter region the cells are more pressed upon by adjoining tissue. In the general epider-

mis, each organ is not only surrounded by the bodies of the epidermal cells, but among these are many gland cells which when distended by their secretion, crowd the structures around them. Thus the cells of the sense-organs in this region must be crowded into a small space. In the cirri, the region in which the sensory cells lie—i. e., the region between the bodies of the epidermal cells and the axial nerve—is filled merely by fibrous connective tissue. The sensory cells in this region, therefore, are less crowded and are generally more elongated—varying from 4 to 12 μ in length and from 1 to 4 μ in width.

Each group of cells has its long axis oblique to the longitudinal axis of the cirrus and the peripheral processes—i. e., the peripheral nerve-fibers—from a given group pass together for a short distance in a course which is oblique to the bodies of the epidermal cells. If the group of cells belongs to a single organ, all the peripheral processes take the same course between these cell bodies. If the group belongs to two or more organs, the bundle of peripheral processes soon separates into two or more smaller bundles which diverge from each other; each smaller bundle then takes its separate course oblique to the bodies of the epidermal cells.

As a given bundle of peripheral processes passes between the bodies of the epidermal cells, it generally becomes slightly less in diameter and bends so that its course is almost at right angles to the cuticula. Quite often, however, the bundle of fibers continues its oblique course until almost to the cuticula, then turns and passes at right angles to it. The peripheral ends of the epidermal cells are thickly covered with brown pigment which does not quite reach the cuticula. In sections the position of the bundle of peripheral processes among the epidermal cells is clearly indicated by the absence of pigment among these processes, so that, wherever such a bundle approaches the cuticula, the band of brown pigment is interrupted by a clear area. It is these clear areas which first catch the eye and enable one to locate the peripheral ends of the sense-organs.

As a bundle of peripheral processes approaches the cuticula, the individual processes separate from one another (Plate

I, Figs. 1 and 2) and the greater number of them branch once or twice (Plate I, Fig. 4 and Plate II, Fig. 35); thus the space occupied by such a bundle just beneath the cuticula is greater in diameter than that at the base of the bodies of the epidermal cells. The entire space is usually somewhat funnel shaped, and the peripheral processes do not always completely fill it. In the latter case, it is clearly seen that the surrounding epidermal cells form an actual stiff-walled cavity. As this was observed in living as well as in prepared material, this cavity is clearly a normal structure (Plate I, Figs. 2, 3, 5A, 13A, 13B and 16).

In the cuticula of a cirrus, over each of these ultimate ends of the peripheral bundles, is a characteristic area which resembles more that over the sense-organs of *Lumbricus* (see Cerfontaine, '90 and Langdon, '95) than that over the sense-organs of the body epidermis of *Nereis*. As seen in surface views such areas do not show the delicate striations of the rest of the cuticula. Near the center of each of these areas are from 5 to 20 minute irregularly grouped pores through which the sensory hairs pass to the exterior (Plate I, Fig. 6). In longitudinal sections of the epidermis, it is seen that the outer layer of the cuticula is apparently lacking over this area—the perforated membrane through which the sensory hairs pass, in the cephalic cirri as well as in the body-wall, appears to be formed entirely from the inner cuticular layer (Plate I, Figs. 5A and 16). In the cirri, however, the absence of the external layer of the cuticula does not produce an external depression such as is found over a diffuse sense-organ in the body epidermis. The outer surface of the perforated membrane in the cephalic cirri is generally more or less convex so that the surface of the cuticula over one of these areas is either plane or actually elevated, rarely concave. The perforated membrane of a sense-organ in the cephalic cirri is only $1\ \mu$ thick and the inner cuticular cavity beneath it is but $2\ \mu$ deep.

In the minute canals which pierce this perforated membrane, lie the ultimate tips of the peripheral processes, each bearing a stiff sensory hair which normally, as may be seen in living cirri, projects some distance above the cuticula (Plate I,

Fig. 3 and Plate II, Fig. 36). The living nerve-cells have a rather coarsely granular central protoplasm surrounded by a clear outer neuroplasm. The same parts may be seen in both central and peripheral processes, each of which has a granular axial strand and a clear outer neuroplasm. The sensory hair itself contains no trace of the granular axial part but appears to be composed entirely of somewhat rigid neuroplasm; or it may be that the extreme peripheral end of each sensory cell, like that of each of the epidermal supporting cells, is actually cuticularized. That the sensory hair is not attached to the general cuticula but is a prolongation of the peripheral process itself is shown by the fact that, whenever a contraction of a peripheral process takes place, the sensory hair is always drawn partly or wholly beneath the cuticula (Plate I, Fig. 4). In the methylene blue preparations, the peripheral processes are often varicose; a large swelling may form at a point where one peripheral process branches (Plate II, Fig. 35) or the sensory hair itself may be swollen into a ball which lies on the external surface of the cuticula (Plate I, Fig. 4). This may even happen to all the sensory hairs in one group and then the entire group appears above the cuticula as a crowded group of spherical bodies (Plate I, Fig. 20). It must be born in mind, however, that these varicosities and swellings are all artefacts.

The central processes from the cells of the diffuse sense-organs present exactly the same appearance as the peripheral ones. The central fibers from one group of cells pass, either alone or after joining those from other groups, to the longitudinal axis of the cirrus and enter the axial nerve (Plate I, Fig. 1). The center of this nerve contains the central processes or nerve fibers from organs lying in the tip of the cirrus; passing toward the base, each organ adds its fibers to the outer surface of the nerve in its neighborhood, and the outermost fibers of the nerve at its base thus come from the organs lying in the base of the cirrus. Generally the fibers enter the axial nerve on the side on which their cells lie, but occasionally they cross the axial nerve and enter it on the opposite side.

The diffuse sense-organs of the anal cirri as seen in hæmatoxylin preparations are exactly like those of the cephalic cirri. Owing to the fact that the caudal end is broken off by the contortions of the worm when injected it is difficult to obtain methylene blue preparations of this region.

In the tentacles and the retractile tips of the palps the sensory cells are also grouped into definite sense-organs which are practically like those of the cephalic cirri. Because of the smaller size, however, of the tentacles and palps, their sense-organs have less room and the sensory cells are, therefore, crowded toward the median axis of each appendage, thus giving rise to what appears to be a crowded mass of isolated cells. It can be seen, however, that each modified cuticular area is supplied by peripheral processes from several sensory cells, thus plainly showing the grouping of these cells into definite organs (Plate I, Figs. 14 and 15.)

In sections of the *palp*, it is a little more difficult to locate a bundle of peripheral processes in its cavity among the bodies of the epidermal cells because the latter, instead of stiffly outlining this cavity as in the cephalic cirri, press closely against the bundle of processes (Plate I, Fig. 15). The modified cuticular area over a sense-organ in this region, as seen in sections, differs from that of the cephalic cirri in but one point—the inner cuticular layer is thinner in the palps thus rendering the concavity beneath the perforated membrane more shallow than in the cirri. A surface view of this cuticular area presents several differences. The pores through which the sensory hairs pass are smaller and more numerous—varying from 8 to 21 in number—and they form an almost circular group.

Each of these groups is in some preparations of the removed cuticula surrounded by a number of larger pores which resemble gland pores (Plate I, Fig. 8). Sections through the palps, however, show that not only are there no glands whatever in the tips of the palps but that there are no canals in the cuticula aside from those through which the sensory hairs pass—i. e., those which lead to the central group of minute pores seen in a surface view. A discussion of these larger pores will be left until the anchoring cells found in the epidermis are described.

In the tentacles, the cells of the diffuse sense-organs lie in some cases among the basal parts of the bodies of the epidermal cells. Many of the sense-cells, however, especially in the distal half of the tentacles, lie in the median axis of the latter. It thus happens that the central fibers from these organs do not form a distinct nerve until the base of the tentacle is reached. In sections of the tentacles it is even more difficult than in the palps to locate the position of the epidermal cavity containing each bundle of peripheral processes. It will be noted that in the cephalic cirri (Plate I, Fig. 5A) the peripheral ends of a few epidermal cells are found attached to the cuticula just within the margin of the inner cuticular cavity. In the tentacles this is carried so far that very slender peripheral ends of epidermal cells almost fill both the epidermal and cuticular cavities and are attached to the cuticula up to and even among the peripheral processes of the sense-cells (Plate I, Fig. 14). As these cell ends are pigmented, their presence under the perforated membrane obliterates the clear area that rendered it easy to distinguish the position of the epidermal cavity in the cephalic cirri.

Around each cuticular area, as seen in the removed cuticula, is found the same arrangement of groups of larger pores that is found in the palps (Plate I, Fig. 8).

In the gill-lobes, the diffuse sense-organs are scattered and each contains but a few cells whose bodies always lie in the epidermis. The modified cuticular area over each sense-organ is exactly like that found in the cephalic cirri.

In the parapodial cirri, large numbers of bipolar nerve-cells are stained by the methylene blue and at first sight appear to be isolated cells. But a study of the removed cuticula reveals the groups of fine pores in modified cuticular areas which enable one to identify the diffuse sense-organs with certainty.

In sections of the *ventral parapodial cirri*, it is clearly seen that the peripheral processes from a few nerve-cells join each other and pass through a slender epidermal cavity to a single modified area in the cuticula (Plate I, Fig. 5B). The bodies of these cells always lie some distance apart and thus give, in sur-

face views of an entire cirrus, the appearance of isolated cells. In sections of the *dorsal parapodial cirri*, there is sometimes found what appears to be a case of isolated sensory cells (Plate I, Fig. 7). It should be noted, however, that each epidermal cavity appears large for a single peripheral process; that the tip of the latter does not show any sign of branching into several sensory hairs as would be necessary if a single cell supplied one of the perforated membranes which, so far as I have been able to determine, always contains several canals; and that, in one of the epidermal cavities figured, a second peripheral process can be seen, although neither its peripheral end nor its cell-body appears in the section. These sections were so faintly stained that one could not determine whether or not other processes were present in the epidermal cavities. In some sections of a dorsal cirrus stained with Kleninberg's hæmatoxylin, the sensory cells appear plainly grouped into definite organs (Plate I, Fig. 17). In my study of sensory hairs in living dorsal cirri, I have sometimes seen such an appearance as that figured in Plate I, Fig. 23. It will be seen that, near the base of this cirrus, some of the sensory hairs appear to be isolated. But in other dorsal cirri, all of the sensory hairs along the same margin were clearly arranged in groups (Plate I, Fig. 18). It must be either that all of the sensory cells of a dorsal cirrus—except perhaps those supplying the extreme tip—are grouped into definite sense-organs and the apparent cases of isolated cells we owe merely to irregularities in the stain or to the destroying of some of the sense-hairs; or else that cirri from the same metameres in different worms or from different metameres in the same worm vary—some having all of the cells grouped into definite sense-organs and some having the cells at the base isolated. From the evidence in hand I am inclined to the former view. In the tip of both dorsal and ventral cirri, as seen in living material, there always appears to be a few short isolated sensory hairs. I have not yet obtained sections or mounts of the removed cuticula which would enable me to verify this observation. In the tips of the cephalic cirri, which are homologous with the parapodial cirri, it can plainly be seen that the

sense-hairs are in definite groups, thus indicating the presence of definite organs (Plate II, Fig. 36).

In these parapodial cirri, the sensory hairs always project a very long distance above the cuticula (Plate I, Fig. 27). In a dorsal cirrus only $300\ \mu$ wide at its base and having a cuticula only $2\ \mu$ thick, the sensory hairs on its dorsal border, as seen in living material, were $32\ \mu$ long and those on its ventral border from 24 to $28\ \mu$. The length of these hairs decreased toward the tip of a cirrus; at the tip itself they were only from 4 to $6\ \mu$ long.

It will now be seen that, with the exception of the doubtful cases in the tips of the dorsal and ventral parapodial cirri and the doubtful cases occasionally seen in the base of a dorsal cirrus, *the sense-cells found in the appendages of Nereis virens, like those found in the body-wall, are all grouped into definite sense-organs. Moreover, since these tactile appendages are purely epidermal outgrowths, it will also be seen that all of their sense-organs, and therefore all of their bipolar sensory cells are situated in the epidermis itself.*

B. Study of the Living Diffuse Sense-Organs.

The diffuse sense-organs of the cephalic and parapodial cirri of *Nereis virens* are excellent objects for a study of living nerve-tissue. If a cirrus be removed from a living worm, mounted quickly in sea-water under a cover-glass, and examined immediately, with the oil immersion, the living nerve-cells, nerve-fibers, and sensory hairs may be studied before any appreciable change takes place in them.

The living nerve-cells of the diffuse sense-organs are more elongated and smoother in outline than are the same tissues after fixation by reagents. Each cell always tapers more or less gradually into both processes (Plate I, Fig. 12)—the rounded form with abruptly attached processes which is so often seen in sections does not appear in living material. As the tissue dies, there appears a tendency for the entire cells to shorten and widen under the action of surface tension.

Living nerve-fibers, while sometimes varying slightly but always gradually in diameter, are comparatively cylindrical and even in outline; they never show any of the varicosities so pronounced in fixed tissues. These varicosities, whether large or small, are always artefacts and never appear until the tissue is dying. They then form in such tissue whether it has been treated with reagents or not. As the tissues die, the nerve-fibers begin to shorten and widen. Occasionally this takes place through some considerable portion of its length, causing an abnormal thickening of the fiber through this part. Usually a nerve-fiber is affected at numerous isolated but often adjacent parts; this causes the fiber to become finely beaded or coarsely varicose, or even, if the contraction goes far enough, to become broken up into a row of disconnected granules. The last condition is more likely to be found in very delicate fibers. If a pigment granule is present in the neuroplasm of a nerve-fiber, a varicosity is apt to form around it. A slight but normal enlargement of a nerve-fiber is apt, during post-mortem changes, to become a large varicosity.

The living sense-hairs are best studied in the parapodial cirri. It can be seen that each living sensory hair is of uniform diameter throughout and has a bluntly rounded apex free from any enlargements whatever (Plate I, Fig. 27). As particles hit against the living hairs, the impulse given by the blow causes a sidewise movement of the sensory hair which is struck. *I never saw anything that I could interpret as a normal withdrawal of one of these hairs.* Since the nerve-cells bearing these hairs lie in the removed cirrus, it seems probable that the removal of the latter does not cause any immediate disturbance of the normal action of the peripheral processes of these cells. As the tissues die, the sensory hairs are often withdrawn, but *always through the formation of varicosities in the peripheral processes.* Often the tips of the sensory hairs swell into a rounded knob (Plate I, Figs. 4 and 24). Sometimes a hair can be seen to form a knob at its apex and then to be slowly withdrawn until this knob rests upon the cuticula (Plate I, Fig. 26). In living tissue stained by methylene blue it can be seen, in such

a case as that just mentioned, that this withdrawal is caused by a swelling of the peripheral process just beneath the cuticula. The part of the sensory hair withdrawn beneath the cuticula often enters into and helps form this varicosity. Sometimes, but more rarely, the apex of this sensory hair remains normal but the base enlarges (Plate I, Fig. 25). In very many cases the formation of a varicosity or the thickening of a considerable portion of a peripheral process withdraws the sensory hair and then the apex swells into a rounded knob (Plate I, Fig. 7). If ammonium picrate or Bethe's fluid be run under the cover-glass upon these sensory hairs while they are still in the normal condition, the same changes take place in them, but more quickly.

It seems to me possible, after seeing the normal form in living tissue, watching the actual formation of these artefacts, and afterward observing their appearance in sections, that such artefacts have been in the past described as normal structures. It appears to me especially desirable that those cases in which a peripheral process from a sensory cell is described as ending in a little knob just beneath or in the cuticula, should be re-investigated—if possible by means of living material.

I consider I am amply justified in deciding that *in Nereis virens every varicosity or beading found in the peripheral processes of the bipolar nerve cells or any end-knobs found on their sensory hairs are artefacts produced during post-mortem changes*. Normally these processes, or nerve-fibers, are cylindrical and almost uniform in diameter and the sensory hairs are cylindrical, bluntly pointed rods which always project above the external surface of the body.

Allen ('94) made a study of the varicosities in the nerve fibers of Crustacea and explains their formation as follows: "Both the phenomena of beading and the formation of end-swells appear to be due to a simple physical cause, namely the difference of surface tension between two fluids. A fluid cylinder surrounded by some other fluid of different surface tension is in a state of unstable equilibrium and tends to break up

into spherical drops." Allen evidently considers that the entire nerve-fiber takes part in the formation of these varicosities; both Dogiel ('93) and Huber ('97) have called attention to the fact that in vertebrate nerve-fibers it is the neuroplasm alone which swells under the influence of post-mortem changes and forms varicosities on the more resistant axial strand. In my own work with *Nereis*, I have been able to see that in the nerve-fibers it is usually the neuroplasm alone that forms these varicosities. Since the granular axial strand is lacking in the sensory hairs it must be that here also it is the neuroplasm that swells when death allows surface tension to act.

C. Course of the Central Processes to the Central Nervous System.

As before stated, the central processes of the diffuse sense-organs found in the body epidermis, including those in the base of the cephalic cirri and palps, were but rarely stained for any distance. It has, therefore, been impossible in my methylene blue preparations to trace these central processes directly into the central nervous system. In a few cases these processes could be seen to enter the nerves in the base of the epidermis. In the prostomium these epidermal nerves pass to the brain; in the rest of the body to the ventral nerve-cord in the metamere in which the epidermal nerve in question is situated.

In the various appendages, the central processes were so well stained by the methylene blue that they could be traced directly into special ganglia or into the brain itself.

The nerves from the anterior or internal pair of cirri pass into a small ganglion which is situated on the circum-œsophageal commissure just ventrad to the point at which this commissure divides into its larger dorsal and ventral roots. The nerves from the posterior or external cirri pass to a second ganglion slightly latero-ventrad of the first. From this ganglion a separate nerve passes to the anterior end of the sub-œsophageal

ganglion.¹ The central nerve fibers from the diffuse sense-organs of a cephalic cirrus can be traced directly through the axial nerve of the cirrus in which they lie into the ganglia at its base and seem to have a definite connection with the cells of the latter structure.

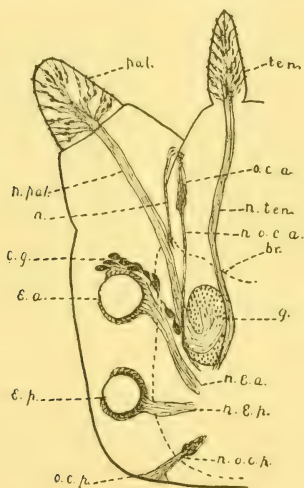
The central processes from the diffuse sense-organs of the tips of the palps pass into the axial nerve of the palp. Each of the two palp-nerves passes to the anterior projection of the brain which lies on its own side. Each then passes directly to the caudal part of the lateral margin of a palp ganglion—a mass of minute ganglion cells situated in the cephalic half of each side of the brain,—and finally mesad and cephalad into this mass of cells. (See Text-figure 3).

Retzius ('95) has figured and described a mass of minute cells—which he calls “vordere Haufen groben Korner,” just in front of each anterior angle of the brain, but entirely outside of it. Racovitza ('96) considers that each of these “Haufen” is composed of two ganglia—“ganglions palpaire et ganglions antennaires,” and that they are in the brain itself. Hamaker ('98) likens the “Haufen” of Retzius to merely the “ganglions antennaires” of Racovitza. He evidently doubts the connection of these bodies with the tentacles and considers them equivalent to the “mushroom bodies” of the insect brain, bodies which are supposed to be the center of control of intelligent action. I have not yet had time to make a thorough study of the brain itself; but from

¹ A point which, so far as I know, has not been previously noted is that this nerve—the “accessory connective” of Turnbull ('88)—is possibly a complete connective—a second circum-œsophageal commissure. From the second cirral ganglion, in which this connective has been described as ending, a nerve which appears to be a continuation of the accessory connective, passes through the first ganglion and, just dorsad of the latter, joins the dorsal border of the circum-œsophageal commissure or primary connective. In the dorsal border of this connective, the nerve in question can be traced for a short distance toward the brain, but finally the sheath separating it from the rest of the connective disappears, although the bundle of fibers seems to retain its original position. Just after this the primary connective gives off its dorsal root *from its dorsal border*. It may be possible that this dorsal root is simply the nerve from the cirral ganglion. In this case the “accessory connective” would be a complete connective passing from the sub-œsophageal ganglion to the brain. In a recent article, Hamaker ('98) notes the nerve connecting the two cirral ganglia, but does not note its further course. He also describes a second, very slender, dorsal root passing from the commissural ganglion into the brain. I am not able to state whether this also appears to be a continuation of the accessory connective.

what I have incidentally observed in some richly stained methylene blue preparations, I judge that Retzius' "vordere Haufen" are merely the palp ganglia mentioned above—ganglia connected only, so far as I can determine, with the retractile tips of the palps. There is no doubt that they are included within the limits of the brain.

The diffuse sense-organs of the tentacles send their central processes into the axial nerve of these appendages and each of these nerves passes to the anterior border of the brain farther dorsad and nearer the median line than does the axial nerve from the corresponding palp. On entering the brain, each passes



Text-figure 3. A diagram of the left half of the prostomium showing the course of the nerves from the tactile appendages and the special sense-organs into the brain.

br., outline of brain; *c. g.*, large ganglion cells which lie beside the anterior eyes and in the adjoining region of the brain; *e. a.*, anterior eye; *e. p.*, posterior eye; *g.*, mass of small ganglion cells to which the palp nerve goes; *n.*, nerve from the supposed sensory area on the base of the palp; *n. e. a.*, nerve from the anterior eye; *n. e. p.*, nerve from the posterior eye; *n. o. c. a.*, nerve from the anterior paired cephalic organ; *n. o. c. p.*, nerve from the posterior paired cephalic organ; *n. pal.*, nerve from the palp; *n. ten.*, nerve from the tentacle; *o. c. a.*, anterior paired cephalic organ; *o. c. p.*, posterior paired cephalic organ; *pal.*, palp; *ten.*, tentacle.

around the median side of the palp ganglion of its own side and appears to enter a mass of large ganglion cells just caudad of the latter.

All the nerves containing the central processes of the diffuse sense-organs found in the various lobes of a parapodium join into a main trunk which passes into the parapodial ganglion situated near the base of each ventral parapodial cirrus. From this ganglion a nerve passes directly to the ventral nerve cord of its own metamere.

D. Ultimate Endings of the Central Processes.

From the foregoing description, it is seen that the central processes or nerve-fibers from the diffuse sense organs situated in the various appendages of the body may either be traced directly into the central nervous system or into peripheral ganglia connected with the central nervous system. The central nerve-fibers from the organs found in the body epidermis without doubt also pass into the central nervous system, but this cannot be so readily demonstrated. The final termination of all these central processes is a question which cannot be definitely decided by means of my present material.

In my methylene blue preparations, large numbers of the ganglion cells in the ventral nerve-cord, in the brain, and in the ganglia at the base of the parapodia and the cephalic cirri are surrounded by *apparent pericellular nerve-baskets*. I use the term *apparent* advisedly for I feel yet undecided whether all or any of these structures are normal. Most of the ganglia in which these baskets are found probably receive other centripetal fibers besides those from the diffuse sense-organs. But in my preparations the central processes of these organs are the only centripetal fibers which are stained. Moreover, two of the ganglia which show these apparent baskets—the two palp ganglia in the anterior part of the brain—receive, so far as I can see, only centripetal fibers from the diffuse sense-organs. Therefore, if proved normal, these pericellular baskets would be without doubt the final terminations of the central processes from the diffuse sense-organs.

These pericellular baskets are apparently formed of deep blue branching and anastomosing fibers which lie within the capsule of the enclosed ganglion cell either just on or above the surface of the latter (Plate II, Fig. 39). The individual fibers are generally beaded or coarsely varicose and closely resemble the nerve-fibers in these same preparations. Sometimes an apparent nerve-fiber can be traced along the axis cylinder of the ganglion cell and directly into one of these pericellular baskets (Plate II, Fig. 40). In all cases in which the wall of the enclosed ganglion cells is wrinkled, the fibers of its basket are situated upon the summit of the folds due to this wrinkling. When the basket is but little more deeply stained than the cell itself, this apparent network is probably the optical section of the wrinkles. In other cases the difference in depth of color between the stains of the walls of the ganglion cell and that of the pericellular basket is too great to be accounted for by a mere fold of the former. If one looked through a pale blue membrane so wrinkled as to show anastomosing ridges separated by intervening depressions, the colored material through which the light would pass to meet the eye would be of greater depth in the ridges than in the depressions between them. This greater depth in material would give a proportionally greater depth in color.

At Professor Reighard's suggestion, I tried an experiment which seems to show that such an explanation as the above will not account for the apparent dark network lying on the surface of a light colored ganglion cell. I placed under the microscope a pale blue ganglion cell which was surrounded by a dark blue network. I then took a thin-walled glass tube and poured into it enough of a light-colored methylene blue solution to give, when one looked into the tube and consequently through the depth of fluid, just the pale blue color of the cell wall. After noting the depth of this solution, I poured in enough more of the solution to give just the deep blue color of the network and compared it with the first mentioned depth. I then measured the thickness of the cell wall itself and that of an apparent fiber of the network. If the apparent fiber were a ridge of the cell

wall, it would seem as if the ratio between its depth and that of the cell wall should be the same as that between the two columns of fluid in my tube. I found that a given fiber of the apparent network was of the same depth as the cell wall itself. If the fiber were the summit of a ridge, the depth of the ridge would then be twice the depth of the cell wall. Therefore, if we overlook for the moment the possibility of refraction, the depth of the stain in the glass tube necessary to produce the same depth of color should be just twice that which gave the color of the wall itself. But the depth of fluid in the glass tube which gave the color of the network was 25 times that which gave the color of the cell wall. The experiment was repeated on other cells with practically the same result. If the greater depth of color in this apparent network were due to refraction, changes in the light and in the focus would render the color brighter; but these changes produce no effect in the depth of color and, therefore, the latter can not be due to refraction. Moreover, it sometimes happens that a dark blue network is found around a cell whose wall is stained pink by the secondary stain. There must be, therefore, some normal or artificial structure along the summit of the folds which of itself, takes a much deeper stain than the cell wall.

An appearance exactly resembling this network is often seen on the varicosities of the nerve-fibers where a pericellular nerve-basket certainly does not normally exist. After my experience in studying living, normal nerve-tissue and in observing the formation of artefacts during post-mortem changes—artefacts that have in the past been considered normal,—I feel that I am not prepared to discuss the question as to whether this basket-like appearance is an artefact in all cases or is a normal structure in the one case and an artefact in the other until I am able to investigate the subject in living material. In my mounted preparations, I can select a ganglion cell which one would say was without doubt surrounded by a terminal nerve-basket. I can select others in which one would instantly decide that the basket was an artificial appearance due to the wrinkling

of the wall. I can also find cells which show all gradations from one of these conditions to the other.

I can, therefore, at present only offer the two following statements :

1. If the appearances described above are pericellular nerve-baskets, some, if not all, of them are the final terminations of the central processes from the diffuse sense-organs. The fibers of these baskets must then strengthen the wall of the ganglion cells with which they are in contact so that these parts, upon the wrinkling of the cell wall become the summits of folds, and the apparent baskets found in other cases—i.e., on varicosities—must be artefacts which further study will enable one to clearly distinguish from the true structure.

2. If the appearance described above is not a pericellular nerve-basket, it is due to the formation of an artificial network in or on the wall of the ganglion cell and this network must differ chemically from the wall so that it takes the blue stains with greater readiness than does the wall itself.

E. Distribution.

A study of the distribution of the diffuse sense-organs by means of the modified cuticular areas as they are seen in a surface view of the removed cuticula and a comparison of the results of this study with the form of the body of *Nereis* reveals several suggestive facts. (See Plate III, Fig. 50.) The anterior end of the body, which is naturally more exposed to contact, is supplied with a very large number of sense-organs. All portions of the surface that lie in grooves and are thus protected by their position are entirely destitute of sense-organs. Those portions that are protected by a position near special tactile appendages are sparingly supplied with sense-organs; for instance the organs are very numerous over the cephalic metameres but become very few on the caudal ones because the caudal end is so narrow that both dorsal and ventral surfaces are protected by the relatively large parapodial cirri. Those portions of the body that have a uniform surface have a uniform distribution of their sense-organs; both the dorsal and ventral surfaces of the

caudal metameres are uniformly level and their sense-organs have, therefore, a uniform distribution; in metameres 6-20 the ventral line is depressed and the sense-organs are, therefore, fewer in the mid-ventral line and more numerous on the raised areas on either side.

The preceeding observations enable one to formulate the following general law of distribution: *The number of sense-organs with which a given portion of the body is supplied is directly proportional to the degree to which this surface is exposed to mechanical stimuli—that is, to the extent of its elevation above surrounding parts.*

The distribution of the diffuse sense-organs in the various parts of the body in accordance with the preceeding law may be summarized as follows:

1. Numerous sense-organs are irregularly scattered over the entire surface of all the special tactile appendages—the cephalic, anal, and parapodial cirri, the retractile tips of the palps, and the tentacles. (See also Plate I, Figs. 19 and 21 and Plate III, Fig. 51.)

2. Over the bases of the parapodia and of the cephalic and anal cirri and over the gill lobes the organs are few in number. The dorsal surfaces of the enlarged bases of the palps are supplied with a very large number of organs; the ventral surfaces contain a very small number.

3. The dorsal surface of the prostomium contains numerous irregularly arranged organs—about 400 in all—of which those on the anterior portion are fewer and smaller. On the ventral surface of the prostomium the organs are smaller and fewer in number.

4. The peristome contains a very large number—about 3600—of sense-organs. These organs are irregularly scattered over the surface in broad irregular bands which pass obliquely cephalo-caudad across the peristome and are limited by the grooves which mark its surface. The sense-organs are more numerous on the dorsal and larger on the ventral surface. They are both larger and more numerous around the anterior than around the posterior part. Around the anterior margin of the

ventral surface is a comparatively wide band entirely destitute of sense-organs.

5. That part of the buccal cavity which corresponds in position to the peristome and which is protruded when the animal is feeding contains a small number of very large sense-organs. Their distribution is practically the same as that in the peristome.

6. In the first metamere the sense-organs are more uniformly distributed than in the peristome. They are somewhat more numerous on the dorsal than on the ventral surface and are less numerous around the parapodia.

7. Passing caudad from the first metameres the following changes in distribution take place :

a. In each succeeding metamere, the organs become very gradually fewer in number up to and including the last caudal metamere. In metamere 41 there are only 1100 organs as against 2000 in the first metamere. In a few of the anterior metameres this decrease in number is accompanied by a decrease in size.

b. There are more sense-organs on the ventral than on the dorsal surface in a few anterior metameres. This difference becomes gradually less to about metamere 12 at which it disappears.

c. The sense-organs extend close to the posterior border of each metamere but are lacking over a narrow zone extending around the extreme cephalic border.

F. Function.

I do not find in the literature any experimental work on these sense-organs, neither have I been able to carry on such work myself. The parapodial, anal, and cephalic cirri, the tentacles and the retractile tips of the palps, from the way in which they are used, have always been regarded as tactile. *Nereis* possesses true eyes and other paired cephalic organs which probably serve for other special senses ; it therefore seems to me that all of the diffuse sense-organs probably belong to the class of tactile organs. Those situated in the appendages and

therefore in the more exposed parts of the body probably receive stimuli for the most part through direct contact with external objects. Those situated in the body epidermis can probably, if necessary, function in the same way, but it seems more probable, since the surfaces in which they are situated are more or less protected by appendages and since their sense-hairs project but little above the general level of the body, that their function is to receive tactile, or possibly chemical stimuli, through the medium of the water. Nereis, when it leaves its burrow, is greedily eaten by various other marine animals. The motions of such animals in its neighborhood and perhaps the chemical substances thrown off by them may be conveyed to it through the water in advance of the animal and may thus enable Nereis to escape the threatened danger. The sense-organs found in the buccal cavity probably serve as gustatory organs.

The method by which mechanical stimuli are conveyed to the cells of the diffuse sense-organs appears to be as follows: If a living cirrus be watched under the microscope, it can be seen that, when a foreign body comes in contact with a sensory hair, the latter is bent passively to one side. This movement may be conveyed to the nerve-cell in one of two ways. Either the passive movement seen in the sensory hair is not confined to this part alone, thus mechanically stimulating the nerve-cell itself; or else the movement of the sensory hair causes a mechanical irritation of the end of the peripheral process on which it is borne, and this impression is conveyed to its cell by the protoplasm of the process as a nerve impulse—that is, each peripheral process is a nerve-fiber. The first method would necessitate a straight, stiff structure capable of purely passive movement. A peripheral process is always so delicate in structure and those in the cephalic cirri are so long and usually reach the cuticula by such an indirect course that it seems to be a mechanical impossibility for it to be a purely passive agent in the conveyance of a stimulus. It would, therefore, appear that each peripheral process, both from its structure, which exactly resembles that of the central processes, and from its probable

method of conveying stimuli from without, must be considered a nerve-fiber.

G. *Summary of the Literature.*

Claparède ('70) seems to have been the first to perceive these sense-organs in any species of *Nereis*. He studied the "terminaisons nerveuses" in "des tentacules, des palpes, et des rames pedieuses" of *N. peritonealis* and *N. cultrifera*. It is difficult to understand his description, but he probably merely saw the sensory hairs in an optical section.

Retzius ('92a and '95) studied the peripheral nervous system of various species of *Nereis*—of which the only one named is *Nereis diversicolor*—by means of the methylene blue and silver nitrate methods. He found a sensory system¹ of isolated, spindle or flask-shaped bipolar cells in the body wall, the parapodia, the tactile appendages and the buccal cavity. His figures and descriptions of these isolated bipolar nerve-cells in *N. diversicolor* closely resemble the bipolar nerve-cells of the diffuse sense-organs of *N. virens*. As before stated, with the exception of a few doubtful cases in the parapodial cirri, I have found that all of these bipolar nerve-cells in *N. virens* are grouped into definite sense-organs. Either two species of the same genus which live practically under the same conditions have the one a sensory system composed of isolated nerve-cells, the other one composed of the same kind of cells grouped into sense-organs or else, as seems to me more probable, the sensory cells described by Retzius are in reality grouped into definite organs. He does not describe any branching of a peripheral process or any especially modified area in the cuticula over these sensory cells, yet it seems probable that he has seen both. In one of his articles (see Retzius, '95, Plate II), he figures without remark a peripheral process which forks in the cuticula and also, in the cuticula above a nerve-cell, the outline of some structure which suggests the ovoid inner cuticular cavity of the sense-organs in the body epidermis.

Retzius describes the peripheral processes as usually ending just beneath the cuticula, sometimes in a little knob. Occasionally he found one ending in a yet finer part which ran partly through the cuticula in

¹ Retzius describes a system of branching nerve-fibers surrounding the setæ-fibers which he believes have no connection with the musculature of the setæ but probably form a second sensory nerve ending. In some of my preparations, these same nerve fibers have been richly stained, but they appear to me to be motor fibers innervating the muscles of the setæ.

a little canal and more rarely he found these finer processes raised above the cuticula. From these various positions in which he found the peripheral end of a peripheral process—beneath, in, or above the cuticula—he decided “dass sie vielleicht beweglich sind; man erhält nämlich den Eindruck, dass sie sich möglicherweise ausstülpen und wieder zurückziehen können.” From my own work, I judge that these finer processes are the sensory hairs of the nerve-cells, that the little canal in which one was occasionally found must be one of the canals of a perforated membrane, that the end-knob in which a peripheral process occasionally terminates is purely an artefact—a varicosity which often forms at the tip of a sensory hair, that normally each peripheral process must project above the surface as a sensory hair, and that the retraction of these processes which Retzius regards as normal must be an abnormal processes—a process which takes place when the tissue is dying and which is usually caused by the formation of varicosities in the peripheral processes themselves.

Retzius states that the greater number of his bipolar nerve-cells lie beneath the epidermis—“die bei weitem grösste Anzahl derselben sich mit den eigentlichen zellenkörper aus der epithelschicht gelöst und in das unterliegende Gewebe eingesenkt hat.” He considers this true, not only in the tactile appendages in which the position of the cells in or beneath the epidermis depends upon one's definition of the limits of the latter structure, but also in the body itself. He considers that this position indicates an advance in organization of the sensory nervous system over that of *Lumbricus* (Retzius, '92b) and, therefore, uses *Nereis* as an illustration of the second stage in the passage of the sensory-cells from the epidermis to the central nervous system during the evolution of the vertebrate sensory system. In the early part of my work, I failed to perceive the true limits of the epidermis in the appendages and therefore fell into the error of supposing the bodies of the sense-cells in the diffuse sense-organs of these structures were “beneath the epidermis” (Langdon, '97). In my later work, I have been able to see that the bodies of the sense-cells in the tactile appendages always lie in the epidermis itself because, as previously stated, each of these appendages is purely an epidermal outgrowth and, therefore, all structures within one of them are in the epidermis, and that the bodies of the sense-cells in the body wall not only lie in the epidermis but generally *even nearer the cuticula than in Lumbricus*. I therefore consider that the sensory nervous systems of *Nereis*, if the position of the bodies of its bipolar nerve-cells can be taken as a criterion, is not higher but lower in organization than that of *Lumbricus* and that there-

fore in any series of animals arranged to illustrate the passage of the sensory cells from the epidermis to the central nervous system, *Nereis* would come before, not after, *Lumbricus*.

Racovitza ('96) states that in *Nereis dumerili* "la surface des deux antennes est hérissée de petits poils sensitifs"—probably the sensory hairs born by the cells of the diffuse sense-organs. He did not investigate these cells.

Hamaker ('98) is the only previous writer who has mentioned the bipolar nerve-cells in *Nereis virens* itself. He figures and briefly mentions *isolated* bipolar nerve-cells which generally lie partly or wholly beneath the epidermis of the body wall and the parapodia. He states that the cells of the sensory fibers of the third parapodial nerve—a nerve which receives the central processes from the diffuse sense-organs situated in the dorsal parapodial cirri and the dorsal gill lobes—"lie far beneath the hypodermis." As before stated, except for the doubtful cases in certain regions of the parapodial cirri, I have always found these bipolar sense-cells grouped into definite organs and, in all cases, have always found the bodies of these cells situated in the epidermis itself. In optical sections of living tissues or in thick microtome sections of methylene blue material, it is very difficult to perceive the unstained cells of a sense-organ and the limits of the epidermis. Even in thin paraffin sections, I have found that I could not feel sure of my results without the use of a secondary stain to define the limits of tissues unstained by the blue. Hamaker does not state from what kind of preparations his methylene blue figures are taken but his failure to use a secondary stain would in itself account for his failure to perceive the true arrangement and position of these sense-cells. Hamaker did not perceive the modified cuticular area over each sense-organ, and although he did not distinguish the sensory hairs as such, he noted that one of the peripheral processes enlarged "just beneath the cuticula into a small knob, from which a fine prolongation extended through the cuticula." This "fine prolongation" is, of course, a sensory hair and the "small knob" an artefact whose formation has partly retracted this hair.

There is a division of opinion concerning the final termination of the central processes from the bipolar nerve-cells—i. e., from the cells of the diffuse sense-organs—in *Nereis*. Retzius ('91) decided that these fibers entered the central nervous system, divided into an anterior and a posterior branch and each branch finally ended in an end-bush. Some of his figures of these end-bushes very closely resemble pericellular nerve-baskets. Among the branches of one of these end-bushes, he

often found an appearance of rounded glistening bodies which, it seems me, might be parts of the surface of an enclosed ganglion cell.

Hamaker ('98) decided that in *N. virens* each nerve fiber of his "set e" is "apparently centripetal, since no cell was found connected with it" and is equivalent to the sensory fibers of *Lumbricus*. These fibers enter the ventral nerve-cord through the fourth nerve, divide into an anterior and a posterior branch, the anterior branch divides again, and all three end in "fibrillations." Moreover some of the branches "lie side by side and are connected with one another by several ladder-like anastomoses." It seems to me unlikely that the sensory fibers should enter the ventral nerve-cord only by one of the five pairs of nerves found in each metamere of *Nereis*—unlikely both from the number and position of these organs and from the fact that in *Lumbricus* their central processes are found in all of the nerves in a metamere.

From his illustrations, I judge that his fibrillations are not the same as the appearances which I have called "apparent pericellular nerve-baskets"—appearances which are often found in the very ganglionic center to which the central fibers of the diffuse sense-organ can be directly traced and in which, as far as I have been able to determine, these same fibers are the only ones in my preparations that are stained by the blue. The mere fact that a given fiber is centripetal does not seem to me to be sufficient evidence that it is the central process from a cell in any epidermal sensory system. From the evidence now at hand it appears to me unlikely that the centripetal fibers described by Hamaker can be the central processes from the nerve-cells of the diffuse sense-organs. It will, however, need a careful tracing, on the one hand, of an individual centripetal fiber of the fourth nerve to its peripheral end, and on the other hand, of an individual central process from a single cell in a diffuse sense-organ to its central end in order to definitely settle this question.

As far as the final terminations of these central processes are concerned, my own observations make it seem possible to me that these will be found to be pericellular nerve-baskets rather than end-bushes or fibrillations.

The only previous accounts of pericellular nerve-baskets in the worms are those given by Retzius ('92c) and Simon ('96) for the leeches. Retzius figures and briefly mentions what appear to be undoubted nerve-baskets around ganglion cells in the brain of *Hirudo* and the ventral nerve-chain of *Aulastomum*. None of the appearances seen by me in *Nereis* have as closely resembled the nerve-baskets of vertebrates as those figured by Retzius. Some of the pericellular baskets figured

by Simon around the ganglion cells of the sub-oesophageal ganglia of the Hirudinea, exactly resemble the appearances found in *Nereis*. As he was not able to find the wall of these ganglion cells, he could not state positively whether the network lay upon the surface of the cell or was embedded in its peripheral protoplasm. Direct protoplasmic communication, however, between the nerve-basket and the ganglion cell, he considers as existing by means of a second, perinuclear, basket which is directly connected with the pericellular one. In *Nereis*, the wall of the ganglion cell may be plainly seen and is often stained; therefore it may be readily demonstrated that the apparent pericellular basket lies outside the wall itself and so far as I have been able to see, has no direct connection with the protoplasm of the enclosed cell. The only appearance I have seen in *Nereis*, which might at first sight be considered a perinuclear basket is one which proved to be the coarse, densely stained, chromatin network of the nucleus of the ganglion cell.

These diffuse sense-organs in *Nereis virens* are strictly homologous with the epidermal sense-organ described in *Lumbricus* by Hesse ('95) and myself (Langdon, '95) and also with those recently described in *Axiotea* and *Clymene* by Lewis ('98). The chief differences between the sense-organs in *Lumbricus* and those in *Nereis* are that in *Nereis* the cells of any one organ are smaller and fewer in number than in *Lumbricus*; in *Lumbricus* each cell bears but a single sense-hair, while in *Nereis* some of the peripheral processes branch and thus bear two or three; the slight concavity in the underside of the cuticula in *Lumbricus* is very much exaggerated in *Nereis* by the increase in thickness of the inner layer of its cuticula so that there results the ovoid cavity which is so characteristic a mark of the diffuse sense-organ of the latter form; in *Lumbricus* the external surface of the cuticula over each sense-organ is elevated, while in *Nereis* it is depressed; and in *Nereis* the perforated membrane appears to be formed only from the inner cuticular layer instead of from both, as in *Lumbricus*.

In *Lumbricus*, which entirely lacks any special tactile appendage, the diffuse sense-organs are apparently the only means the animal has of receiving tactile impressions. Living as it does in a comparatively dry burrow or crawling over the surface of the ground, it may be that it would more easily receive these impressions without injury to the rest of the body if the sensory hairs were borne on an elevated area. Since the surface of *Nereis*, whether in or out of its burrow, is always bathed by the sea-water, the sense-hairs, whatever their position, would also always be surrounded by this medium; stimuli conveyed through

the latter would be, therefore, just as quickly perceived if the external ends of these organs were more or less sunken beneath the surface, and the sensory hairs themselves would be thus better protected from injury. Nereis, as is well known possesses special tactile appendages which probably serve for all cases in which tactile impressions are to be received through actual contact with foreign bodies; the cuticular area over a sense-organ in these appendages resembles that over a sense-organ of *Lumbricus*.

The differences between the "diffuse sense-organs" of Nereis and the "epidermal sense-organs" of *Axiiothea* and *Clymene* are as follows: In *Axiiothea* and *Clymene*, the sense-organs as a rule "vary in size directly with the thickness of the cuticula;" the opposite is true in Nereis. A longitudinal section of the cuticular cavity over the sense-organs of the first named forms resembles more that found in the appendages of Nereis than that found in the body-wall, in that the inner cuticular cavity is shallow and wide at its inner end and the base of the outer cuticular cavity is elevated. As Lewis does not figure the two layers of the cuticula it is impossible to decide whether, as in Nereis, the perforated membrane is formed from the inner cuticular layer. In *Axiiothea* and *Clymene* there is never but one sense-hair to a peripheral process; in Nereis there are sometimes two or three. Lewis considers these hairs probably normally retractile but states that she can give us no proof. She found two sensory hairs stained by the blue which seemed to move for a considerable time and change their position with reference to each other. This, it seems to me, was due to post-mortem changes taking place in the peripheral processes on which these hairs were born and not to any normal movement. She examined the removed cuticula of Nereis and concluded, from the likeness of the surface views of the cuticular areas over the sense-organs to those found over the sense-organs of *Axiiothea* and *Clymene* that similar organs must exist in Nereis.

Blochmann ('95) and Zernecke ('95) have described and figured in the Cestodes and Blochmann and Bettendorf ('96) in the Trematodes a peripheral sensory system of isolated bi-polar nerve-cells lying partly in and partly beneath the sub-cuticular region. The peripheral processes of these cells are described as entering a "birnformigen Hohlraum" in the inner side of the cuticula and ending in this blind cavity in a "nagelkopfähnliche Platte" from which occasionally a small "Stiftchen" passes a little farther into the cuticula. Blochmann and Bettendorf regard this "Stiftchen" as probably always present but generally uncolored. Zernecke believes that, in the

Cestodes, it is probably an abnormal appearance caused by the silver nitrate deposit. All of these workers regard the end-knob of the peripheral process as a normal structure. Zernecke states that above these peripheral terminations in the Cestodes there is occasionally found a depression in the cuticula but does not think there can be any normal relation between the two. That is, according to all of these investigators the peripheral terminations of the bipolar nerve cells in the Cestodes and Trematodes are not external but lie in a small blind cavity which penetrates only the inner one-fourth of the thickness of the cuticula.

It seems to me probable, in comparing these peripheral terminations with those of the diffuse sense-organs of Nereis, that this blind cavity is but the lower part of such a modified cuticular area as has been described in preceeding pages for Nereis¹. It often happens in my preparations that the plane of the section is such that the ovoid inner cavity is cut obliquely (Plate II, Fig. 37). Then not only will the perforated membrane and outer cavity not appear in the section, but the inner cavity itself will often appear to extend but a short distance into the cuticula. In this case the appearance seen is similar to that figured by Blochmann and his pupils in the Cestodes and Trematodes and for some time I thought this appearance showed the correct structure of the cuticula over a sense-organ of Nereis. Even where the entire cuticular area appears in the same section, it is difficult without the use of a secondary stain in the methylene blue preparations to perceive the outer cuticular cavity even when the inner one is clearly defined.

The end-knob described by all these investigators as terminating each peripheral process, I regard as probably a varicosity formed during post-mortem changes—a varicosity whose formation caused the withdrawal of the “Stiftchen” which they occasionally found projecting from it. I believe that this “Stiftchen” is a sensory hair and that it normally passes through the cuticula and projects above the external surface. When the “Stiftchen” is not seen it is probably sometimes, as suggested by Blochmann and Bettendorf, unstained and sometimes wholly withdrawn; in the latter case the end-knob would be the abnormal swelling of the tip of the sensory hair so often found in Nereis. (See Plate I, Fig. 4.)

¹ If the modified cuticular area over the sensory cells of the Cestodes proves to be homologous with that in the cuticula of Nereis, it may be that this homology will tend to prove that the cuticula in the first named form is homologous with that of Nereis and that, therefore, the theory which claims the subcuticular tissue as epidermal is the correct one.

The sensory systems of these worms, as is known to be the case in other worms, would then come into direct relation with the external world—a condition which seems more probable than that this system should receive stimuli through a thick layer of resistant cuticula.

The nerve cells of the sensory system in the Cestodes and Trematodes closely resemble those of the diffuse sense-organs of Nereis. In several cases they are figured so close together that it would not be surprising if further research should prove that in some regions of the body these cells are grouped into small yet definite sense-organs.

Brode ('98) considers the metameric arrangement of the sense-organs of Dero of importance as a proof of the colonial theory of metamerism. My study of the distribution of the sense-organs of Nereis, especially when this distribution is compared with the form of the body and the movements of the worm itself, has led me to the opposite conclusion. The distribution in a given part of the body is so dependent upon the external form of this part and the form is so dependent upon the method of locomotion that I have been led to adopt the theory of Meyer ('91) that the metamerism of worms has been brought about by a secondary segmentation due to muscular activities. A further support of this theory is found in Nereis in that the external and internal metamerism do not agree with one another. It seems to me most probable that in the primitive worm the diffuse sense-organs—or what is probably their earlier form, isolated sense-cells—were evenly distributed over the general body and merely somewhat more numerous at the anterior end. Then as greater size and complexity of body brought metamerism with it through muscular activities, there became apparent a tendency for the sense-organs to become more pronounced in the more exposed portions of a given metamere and a tendency for the disappearance of these organs in regions in which they were of less use. There would thus be brought about a *secondary* arrangement of the diffuse sense-organs in girdles or longitudinal lines. I would therefore not lay stress upon the distribution of these sense-organs as a guide in tracing lines of descent.

V. SPIRAL ORGANS.¹

In the body epidermis, in the bases of the palps and cephalic cirri, and in the gill-lobes of the parapodia, are found com-

¹ These organs were called "ocular organs" in a brief résumé which appeared in Science (see Langdon, '97). I have since thought best to designate them by a term that will apply to them even if further research should prove my present conception of their function erroneous.

plicated epidermal organs to which I have given the name *spiral organs* because of the peculiar spiral arrangement of the peripheral processes of their cells. I have found these organs not only in *Nereis virens*, but also in the living parapodia of a second species—probably *N. limbata*, Ehlers.

A. Structure.

Each organ consists of a slender central tube around which are the spirally arranged peripheral processes from about 100 bipolar or multipolar cells whose bodies generally lie in the epidermis (Plate II, Fig. 41). The central tube and the peripheral processes arranged around it, whether seen in living material or in sections, form the most conspicuous part of one of these organs. This part is nearly ovoid, about $80\ \mu$ long, $40\ \mu$ wide at its widest part, and has its smaller, somewhat pointed end pressed into a small cavity in the under side of the cuticula. This cavity is about $6\ \mu$ wide at the inner limit of the cuticula; from it a tubular opening or canal about $2\ \mu$ in diameter extends entirely through the cuticula, flaring a little at its outer end at which it becomes $4\ \mu$ in diameter (Plate II, Figs. 44 and 47).

The central tube is a cylindrical, flexible, thin-walled structure; it enlarges gradually from its peripheral to its central end and averages $2\ \mu$ in diameter (Fig. 43). The basal end of this tube appears to end blindly, but it is so covered by the lowest peripheral processes that it is difficult to determine this with certainty. The peripheral end of the tube passes into the shallow cavity in the under side of this cuticula above it. In the body epidermis and in the bases of the palps, the apical turn of the spiral formed by the peripheral processes lies in this cavity in the under side of the cuticula just where the cavity passes into the cuticular canal above it (Fig. 41.) In the gill lobes, the cuticula is very much thinner; in this region the apical turn of the spiral lies entirely below the cuticula and it can be seen that the central tube runs up to the cuticular canal and that the lumen of the tube is continuous with that of the canal and therefore opens to the exterior (Plate II, Fig. 43).

Quite often one of these cuticular canals contains a rod-like

body which takes a deeper stain than the inner cuticular layer—a stain like that of the outer cuticular layer. The inner end of this apparent rod joins the apex of the spiral organ; the outer end is sometimes bluntly rounded, but more often flares a little (Plate II, Fig. 45). Careful study seems to show that this apparent rod is an artefact. Very often the cuticular canal appears to be a mere opening through the cuticula without distinct walls of its own; then again it often appears to be lined by a distinct layer which takes a deeper stain than that of the surrounding cuticula. Finally cases are often found in which the lower parts of the more deeply stained lines along the two margins of the canal have separated from the inner layer of the cuticula (Plate II, Fig. 44). It may also be seen, both in sections of prepared material and in the surface views of living material, that the outer layer of the cuticula thins out and dips down into the flaring outer end of the canal; moreover, in macerations, the central tube always remains attached to the cuticula. All of these various appearances have led me to the conclusion that the central tube of the spiral organ passes entirely through the canal in the inner layer of the cuticula, the tube normally being closely pressed, perhaps actually joined to, the sides of the canal. The appearance of a rod in this canal is due to reagents, which cause the outer end of the central tube to shrink partly or wholly away from the cuticular canal in which it lies and to assume a rod-like form. This interpretation is borne out by the fact that this apparent rod has never been found in living material—the central tube always appearing empty throughout its length. The dipping down of the outer layer of the cuticula into the outer end of the cuticular canal suggests that the central tube of the spiral-organ is an invagination of the outer cuticula—an invagination probably formed before the formation of the inner layer of the cuticula. If, as now seems probable, the outer layer of the cuticula is either shed or worn away, the outer end of this central canal must each time either shift its attachment or else the inner surface of the canal itself must disappear and the cells of the spiral organ secrete new cuticular material.

The bodies of the cells of the spiral-organs may be found scattered among the basal processes of the epidermal supporting cells at a considerable distance and in any direction from the base of the central tube and in such cases the basement membrane of the epidermis is continuous beneath the organs. Sometimes, however, the cell-bodies lie in a group more or less directly beneath the central tube (Plate II, Fig. 41) and then the basement membrane of the epidermis is lacking under this group. Its place is taken by a thin membrane whose homology I have not been able to decide. It is formed of slender nucleated strands which resemble much flattened muscle-fibers, and is always convex on its inner surface. Sometimes all the cell-bodies of several spiral-organs lie in the same group and then the membrane under this group is so much curved as to form a sort of pouch projecting centrally. This is always the case in the bases of the palps, in which these pouches often extend beneath the epidermis a distance as great as the depth of the latter.¹ In the gill lobes, the bodies of the cells belonging to a single organ lie in a few groups beneath the central tube among the bases of the epidermal cells.

The body of each cell is quite large; its protoplasm is coarsely granular and its nucleus takes a uniform stain and contains a large nucleolus. The different cells of the same organ vary greatly in form. Some are oval or broadly elliptical bipolar cells, but by far the greater number are irregularly shaped multipolar cells (Plate I, Fig. 22 and Plate II, Fig. 41). All of the processes except two seem to be short slender processes which extend in various directions among the surrounding cells. One of the two longer processes is also slender. In living gill lobes taken from animals that have been injected by the methy-

¹ Retzius ('92a) figures, in the palps of *Nereis diversicolor*, the outline of large "Drüsen" which exactly resemble the outline of one of the above mentioned pouches when a spiral organ appears in the same section and thus continues the outline of the pouch to the cuticula. The glands of *N. virens* are comparatively small and do not project centrally beyond the general level of the base of the epidermis. I at first looked upon these pouches in the palps of *N. virens* as glands and it may be that Retzius has fallen into the same error in *N. diversicolor*.

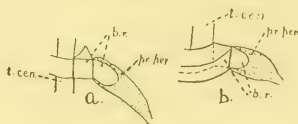
lene blue, this process is beaded or varicose and may be traced almost into one of the nerves of the lobe. It would, therefore, appear that this process is a central nerve-fiber. It may be seen also that consecutive sections always reveal a nerve in the base of the epidermis in the place occupied by several spiral organs in previous sections. There is never any appearance of a nerve passing to the central end of one of the pouches described in the palp, but one is always found passing to one side of its peripheral end. It seems that the central processes, in such a case, must pass peripherally into the base of the epidermis before entering a nerve. Everything indicates that these central processes always enter epidermal nerves but I have never been able to trace an individual process directly into a nerve. In living material the surrounding tissues render this tracing difficult and in mounted methylene blue material, the spiral organs are poorly preserved and have lost most of their stain. Without doubt these central processes in some regions of the body pass to the same ganglionic centers that receive the central processes from the diffuse sense-organs. The fact that they are, in all cases, stained by the blue for only a short distance centrally from the body of their cells would, I should judge, preclude the possibility of any of the apparent pericellular nerve-baskets found in these centers belonging to them. This does not, of course, preclude the possibility that these central processes also end in nerve-baskets—baskets unstained in my present preparations.

The second longer process from one of these cells is the peripheral one first mentioned. This process is always much stouter than the other processes from a given cell and enlarges at its end into a club-shaped part which terminates in a highly refractive body (Plate II, Figs. 41, 43 and 47). The peripheral processes pass toward the surface and at the same time toward the central tube in several small bundles and are generally attached on their own side of the tube. Sometimes, however, a single process, or even an entire bundle passes quite around the central tube and is attached to its opposite side. Either just before or just after enlarging into its club-shaped peripheral end

each process arches toward the central tube and its refractive body appears to be joined to a thick band which is wound spirally around the tube. The protoplasm of these peripheral processes as seen in living material, appears to be made up of transparent semi-liquid drops contained in the meshes of a very coarse, highly refractive network. In a few of my methylene blue preparations, there appears to be a nucleus lying close against one side of the enlarged end of a peripheral process. In material killed by alcohol or Müller's fluid, this appearance is never seen. The highest powers of the microscope and the most careful focusing never reveal any structure in a living peripheral process except the protoplasm previously described and the apical refractive body. As the nuclei in the cell bodies are clearly seen in living material, I believe, if one existed in the enlarged part of a peripheral process, it too could be seen. Moreover, in methylene blue preparations examined when the tissues are living, there is no trace whatever of the apparent nucleus seen in the permanent methylene blue preparations. In the latter, the spiral organs are poorly preserved. Each peripheral process is much vacuolated and its protoplasm is consequently reduced to mere threads or films which are forced against the wall of the process. The apparent nucleus seen in these preparations seems to me to be merely a thicker place of one of these threads.

The refractive bodies are clear, lens-like structures which take the stain but faintly, if at all. Each, when viewed from above, is generally rounded at the end away from the central tube and tapers from this end toward a slender rod-like part which rests upon the outer surface of the spiral band previously mentioned (Pl. II, Fig. 43). These rod-like parts give this band an appearance resembling the rim of a cog-wheel. (Pl. II, Fig. 49 g). The refractive bodies belonging to the peripheral processes, which pass to the deep end of the central tube seem to rest, when seen in living material, directly upon the tube itself. Sections, however, show that the spiral band is also present here, making its last turn around the base of the tube. When viewed from the side, it is seen that each refrac-

tive body really consists of two parts—an ovoid part embedded in the protoplasm of the peripheral process and continuous with a somewhat wedge-shaped block which extends quite to the central tube. (Text-figure 4). It is therefore clear that the spiral band is really not a separate structure, but is formed of



Text-figure 4. Lateral views of the tips of two peripheral processes in a spiral organ. *a* shows a refractive block with a ridge on its upper surface; *b* shows one which lacks this ridge and thus builds a smooth turn of the spinal.

b. r. refractive body; *pr. per.* peripheral process; *t. cen.* central tube.

the wedge-shaped blocks of the refractive bodies, arranged side by side in a spiral manner around the central tube. One of these blocks has usually seven surfaces. (Text-fig. 4, *a*, and Pl. II, Fig. 46). The two lateral surfaces are closely joined to the corresponding surfaces of adjacent blocks. In living material this plane of union is not visible; under the influence of reagents the blocks separate a little from one another and the component parts of the spiral band may then be seen. (Plate II, Fig. 41). The outer surface of each block is continuous with the ovoid part of the refractive body and with the protoplasm surrounding the latter. The lower surface is free and forms the lower surface of the spiral band; the upper surface is also free and usually bears an angular ridge which gives the cog-like appearance previously described upon the outer surface of the spiral. The inner surface of one of these blocks usually consists of two parts; the lower part is concave from side to side and closely joined to the central tube while the upper is free and forms an acute angle with the tube. It is these free upper parts of the inner surface that form the upper border of the spiral band. Sometimes the entire inner surface of several blocks joins the central tube and then the angular ridges on the upper surfaces are lacking. (Text-figure 4, *b*), and the part of the spiral band formed by these blocks appears smooth. In

a side view, the ovoid part of the refractive bodies, often does not show. (Pl. II, Fig. 46). These parts are, however, so generally found in views from above and in macerations that I am inclined to think they are always present; probably when apparently absent, they are concealed by a thick layer of protoplasm. The different appearances presented by these refractive bodies do not seem to be limited to any particular part of a spiral organ or to the organs of a definite region of the body. Occasionally I have seen in the gill lobes peripheral processes which contained refractive bodies of abnormal size or shape or even accessory bodies which were entirely unconnected with the apical one. (Pl. II, Fig. 48). As far as I can judge, these accessory bodies always have the same optical properties as the normal refractive bodies.

The refractive bodies might be either a hardened secretion of the cells with which they are connected or the metamorphosed tips of the peripheral processes. The protoplasm of the peripheral process is usually found to entirely surround the ovoid part of a refractory body and sometimes even the wedged-shaped blocks. This shows that, whatever its method of formation, a refractive body is an inclusion of the cell which produces it.

Under the influence of macerating fluids, the peripheral processes swell and soon go to pieces. The central tube not only remains attached to the cuticula but the refractive bodies remain firmly attached to the tube although component blocks of the spiral band sometimes separate a little from one another. It has therefore so far proved impossible to obtain for study a perfect detached element of a spiral organ—i. e., a cell with all its processes and its refractive body. The small size of the refractive bodies and their peculiar spiral arrangement around a tube of so small diameter produces many optical effects which render difficult the study of these bodies. The foregoing account however contains only descriptions which have been tested by repeated observations.

The spiral band may be either a left- or a right-handed spiral but the two never occur in the same organ. The en-

larged parts of the peripheral processes in consecutive turns of a spiral usually touch each other, but consecutive turns of the spiral band itself are always separated by a space about of the width of the band.

In sections from material killed by alcohol, the peripheral processes appear to be very slender and to be separated by very large clear spaces. These spaces are really enormous vacuoles which have formed within the processes themselves forcing the protoplasm to one side. The strands of protoplasm between these vacuoles thus present the appearance of very slender peripheral process separated by large clear cells (the vacuoles). In some material killed by Müller's fluid, a few of the upper peripheral processes and the cells to which they are attached are much more deeply stained than the lower processes in the same organ. (Plate II, Fig. 41). The protoplasm of such processes always appears more poorly preserved—i. e. more shrunken and more disintegrated—than others. The only explanation I can offer is that this appearance may be due to a different physiological condition of these processes or of the cells which bear them at the time of death. I am certain that it is not due to any morphological difference or to any difference in function. In living material and in some material killed with alcohol no essential difference whatever can be observed between cells or peripheral processes in different regions of a given organ; in material injected with methylene blue, the cells which take the blue may lie in any part of the organ. I therefore consider *that a spiral organ is composed of but one kind of cell and this cell is a nerve cell.*

Pigment is never present either in or around the peripheral processes. It is sometimes found in and among the bodies of the cells belonging to the spiral organs but never in any larger quantities than are found associated with other structures in the base of the epidermis.

C. Distribution of the Spiral Organs.

The number of the spiral organs is comparatively small. They are most numerous on the head; in the body itself they

are apparently confined to the first 20 metameres. The only appendages in which they are found are the gill lobes and the bases of the palps and cephalic cirri.

A reconstruction of the head and first metamere shows that in this region the spiral organs have a definite arrangement which may be summarized as follows. (Plate I, Fig. 28):

1. On the base of each palp about 43 organs are scattered over the outer or lateral surface ; they are entirely lacking on the inner surface.

2. A few organs are found in the outer surface of the bases of the cephalic cirri.

3. On the dorsal surface of the prostomium are two broad irregular bands of 15 or 16 organs each, which extend, one on either side, from the base of the tentacles almost to the anterior eyes. Each of these bands is thus practically in line with the true eyes on its own side of the prostomium. No spiral organs are found on the ventral surface of the prostomium.

4. About 372 organs occur in the peristome in the raised surfaces between the grooves. In the mid-ventral region these organs extend to the posterior margin, but not to the anterior one. Passing dorsad they may be said to be distributed in a wide band which occupies about the median two-fourths of the peristome. In the mid-dorsal region, this band is narrow and is found only at the anterior border. Just caudad of the base of the cephalic cirri this band is extended to the anterior margin by a group of about 33 organs.

5. In the first metamere about 56 organs are found in a narrow median zone which passes over the dorsal and lateral surfaces between the parapodia of opposite sides. Just ventrad of each parapodium is a group of 8 or 10 organs. About 6 organs are found in the anterior half of the mid-ventral region of this metamere.

Although the above statements rest on a study of but one reconstruction, my study of sections of other worms shows that the main facts of distribution must be generally true. Variations in the whole number and exact location of each organ

in a given region always exist in the two sides of the same worm and probably in the same side of different worms.

A study was also made of the distribution of these organs by means of surface views of the epidermis. As the results thus obtained did not appear to be strictly accurate they were not included in the chart. This study, however, tended to show that the median zone of spiral organs occurred in the dorsal surface of every metamere as far back as the twentieth and that the number of organs in each zone back of the first became gradually less.

From a study of living parapodia it was found that the spiral organs are found in the tips of each gill-lobe of every parapodium; the number found in a given parapodium depends directly upon the size of the latter. As many as 15 are sometimes found in a single gill-lobe.

C. Function of Spiral Organs.

The spiral organs of *Nereis* suggest three different classes of organs—compound glands, phosphorescent organs whose structure is similar to ocular organs, and ocular organs themselves.

The component cells of these spiral organs not only differ in structure from the isolated gland-cells in the epidermis of *Nereis virens*, but also when tested by a special stain like Biondi-Ehrlich never take the stain of gland-cells. They always stain more like undoubted nerve-elements. Moreover the most careful study under the oil-immersion has failed to reveal any secretion in the central tube or any opening from a peripheral process into this tube. A refractive body always fills the tip of each process. Sometimes the secretion from one of the mucous gland cells hardens under the influence of reagents in the peripheral end of the cell. But such a hardened glandular secretion always takes an intense stain, while the refractive bodies of the spiral organ remain almost if not quite colorless. Moreover they are found to be hardened structures even in the living condition. As far as present observations go I therefore

consider it impossible that these spiral organs should be glands of any kind whatever.

The phosphorescent organs of some invertebrates have practically the same structure as simple ocular organs. The two have often been mistaken for one another and are supposed to be derived from the same primitive organ. From its structure the spiral organ might belong to either class.

I have not found in the literature any record of phosphorescence in *Nereis*. Moreover, as much as I have worked with the living spiral organs, crushing them in sea-water, exposing them to the air, and watching them for hours under the microscope, I have never seen any trace of luminosity. Experimenters on phosphorescent organs have found that an organ becomes luminous when removed and crushed in water, even, according to Vallentin and Cunningham ('88), in the day time. It therefore seems to me, that the possibility of these organs functioning as phosphorescent organs can be set aside until some direct proof of this function is brought forward.

This leaves the ocular, or at least the light perceptive, function as the only probable one.

The simplest form of ocular organs among invertebrates is that described by Hesse ('95) for the *Lumbricidæ* and closely related forms. Each organ consists of but a single cell. Each cell possesses a basal process which is probably a nerve fiber, a nucleus in its basal end, and an irregularly prolonged peripheral part which contains a refractive body. If one imagined this peripheral process drawn out into a longer process with the refractive body confined to its extreme tip and changed in shape by the pressure of surrounding parts, one would have an individual cell of the spiral organ of *Nereis virens*.

Sharp ('84) has described in *Solen* ocular organs each of which consists of a group of cells arranged around a central invagination. These cells have clear peripheral ends, pigmented middle portions, and a basal part containing a nucleus. Except for the pigment, this would correspond in general with the spiral organs.

Andrews ('91) has studied the "branchial eyes" of several

sedentary Polychætes. He found these organs in *Potamilla* to consist of an area of cells each of which has a basal process, a nucleus in the basal part of the cell, and a larger peripheral process containing a large refractive body. Each refractive body is usually firmly attached to the cuticula. There are sometimes other "inclusions" between this apical refractive body and the nucleus. Each cell is covered with pigment granules. Andrews experimented with these eyes to see if they were phosphorescent organs with but negative results. Here then, in the Polychætes, is a case of a simple eye whose cells closely resemble those of the spiral organs of *Nereis*. If the simple area in *Potamilla* became invaginated, the peripheral ends of its cells spirally arranged, and the bodies of its cells farther removed from the cuticula, we should have, except for the presence of pigment, the spiral organ of *Nereis*.

In a later paper, Andrews ('92) gives an account of the true eyes of many Polychætes. In all of the forms studied macerations showed that the retinal cells were the nerve-cells, that the base of each cell was prolonged into a nerve-fiber, and that the peripheral end bore a slender refractive rod. In the *Syllidæ*, it could be further seen that the lens was made up of the refractive peripheral ends of the retinal cells and that the entire organ was attached to the cuticula by a stalk which probably represented an invagination. There is also strong evidence that the lens of the eyes of all Polychætes is composed of separate elements—elements which are but the transformed peripheral ends of the retinal cells. Andrews' figure of the eye of *Lepidonotus* is strikingly like the appearance shown in a section of a poorly preserved spiral organ. Each of the retinal cells of this form bears a refractive body at its tip and these bodies, closely packed together, constitute the lens.

Hesse ('99) has lately re-investigated the eyes of Polychætes. One of the simpler ones—the "Augenflecken" of *Ranzania sagittaria* in several respects closely resembles the spiral organ of *Nereis*. It has a central solid cylinder which appears to be an invagination of the outer layer of the cuticula and which corresponds to the central tube of the spiral organs.

Closely investing this central cylinder is a clear zone which is continuous with the inner layer of the cuticula and which appears to consist of separate elements each of which belongs to the peripheral end of a visual cell. These elements correspond to the refractive bodies of the spiral organs. Between the bodies of the visual cells and this clear zone is a layer of pigment.

A comparison of the figures and descriptions of these various eyes with the spiral organs of *Nereis* leads me to the conclusion that the latter must be simple epidermal eyes; that their cells are retinal cells; the ovoid and wedge-shaped parts of the refractive bodies, rods and lens elements; and their central tube merely an invagination of the cuticula. These spiral organs need only a close packing of their lens elements and the addition of pigment to be strikingly like the eyes of several of these Polychætes.

The absence of pigment might be taken as evidence against the ocular character of these organs, or at least as evidence that they were not at present functional. However, both Whitman ('89) and Nagel ('96) have arrived at the conclusion that pigment is not a necessary part of a functional eye.

The main difference in structure, besides the absence of pigment, between these spiral organs and the ocular organs previously described is the spiral arrangement of the peripheral processes around the central tube—an arrangement which, so far as I know, has never been described for any sense-organ. This spiral seems at first to be the result of an actual whirling around of the entire cells but the position of the cell-bodies precludes this possibility. In reality I believe this spiral is due simply to two processes which take place during development—the increase in depth of the epidermis by a growth in length of its elements and the sinking of the bodies of the cells belonging to a spiral organ below their former level. In the eyes of Arthropods, Patten ('89) found that the clear refractive tips of the visual cells were hexagonal and fitted closely together. In *Nereis* the outer ends of the epidermal cells are hexagonal and fit closely together. If a tubular invagination of such an area of simple epidermal cells should take place, the invagin-

ated cuticula would form a central tube and the peripheral ends of the epidermal cells, being attached to this cuticula, would arch inward to this tube. The surface of the latter would thus be covered with the hexagonal ends of these cells. If now an increase in the depth of the epidermis should take place by an elongation of its cells and if also the nucleated parts of the cells attached to the tube should grow downward and laterally so as to lie among the bases of the other epidermal cells, there would be two forces pulling upon the peripheral ends attached to the central tube. One force would tend to pull the cuticular tube outward away from the cells attached to it; the other force would tend to pull the peripheral ends of these cells downward away from the tube. If the strain from these two forces continued long enough it would tend to pull the peripheral ends of the cells away from the central tube. As a result of either force it would be the upper part of each process which would first loose its connection with the cuticular tube, because this part is more convex and thus being under a strain due to its own form is less able to resist the downward pull of its own cell-body or the upward pull of the cuticular tube to which it is attached. It will be remembered that, in these organs, there is a space between two adjacent turns of the spiral and that the upper half of the inner face of each component block of the spiral is usually free while the lower half is still joined to the tube. Such a process as that described above would account for both of these—the free upper half of the upper face of the block would be the half of the peripheral end which had been pulled away from the surface of the central tube; the space between two adjacent turns of the spiral would be the space thus left upon this tube, increased probably by a stretching of the thin cuticular tube itself. It will be remembered that some of these component blocks of a spiral bear ridges upon their upper surfaces while some are smooth. This is probably to be accounted for by the fact that all of the cells in any epidermal area are not true hexagons. In some cases it may also be accounted for by the possibility of some of the refractive blocks being still in a plastic condition when the separation

above described takes place and thus being still able to change their form under the influence of surface tension and also of external forces.

When the upper halves of the peripheral processes became pulled away from the tube, they would also be separated from the lower halves of the processes next above them *and this line of separation would be a line passing spirally around the central tube.* The truth of this statement can be easily demonstrated. If a surface be covered with hexagons, it will be at once seen that the line of least resistance—the line along which these hexagons would most easily separate—is an oblique one. If the surface of a thin plate of clay be marked with hexagons and the plate carefully invaginated so that the hexagons are on the outer surface of the invagination, and then a line be traced through the hexagons along the line of least resistance, *this line will pass spirally around the invagination and if the hexagons are very small, it will need but one such spiral to take in every hexagon on the invagination.* This shows that in an invaginated surface formed of small hexagonal cells, the line along which these cells will tend to break apart under strain is a spiral one winding around the invagination. This, it seems to me, accounts for the spiral arrangement, characteristic of the spiral organ.

The above explanation needs to be tested by a study of the development of these organs. It is, however, an explanation built upon general facts of development, for it will be conceded that ocular organs come from simple epidermal areas which often become invaginated, that epidermis increases in height during development, and that the bodies of epidermal cells, especially nerve-cells, often wander from their original positions. The truth of the mechanical principle involved can easily be tested. In ocular organs of other forms in which the refractive bodies are massed together, the cell bodies lie close to the refractive bodies and there has been no change of position which would cause the refractive bodies to separate from one another.

The position of these spiral organs on the dorsal and lateral surfaces of *Nereis* and in the tips of the gill-lobes is that

best suited to enable these worms to receive luminous impressions from above and from either side—as would be necessary when they leave their burrows. The greater number of these organs on the prostomium, palps, and peristome and also their presence on the ventral surface of the peristome would be a great protection when the animal simply thrusts its head from its burrow. Since *Nereis* possesses true eyes, these spiral organs probably serve, not for the perception of distinct images, but of difference in intensity of light. Nagel ('96) has shown that animals which lie buried in the sand with only a small portion of their body exposed have this portion supplied with ocular organs. Experiments show that, in such cases, this part is extremely sensitive to differences in intensity of light and is quickly withdrawn when a faint shadow is cast upon it. Nagel therefore concluded that these organs give warning of the approach of enemies by the perception of their shadows. In the absence of direct experiments on the spiral organs of *Nereis* it may be concluded that the general explanation given by Nagel is also applicable to *Nereis*—that the spiral organs are ocular organs which have for their function the perception of differences in intensity of light.

VI. *Paired Cephalic Sense-Organs.*

A lack of the necessary material and time has prevented me from making a thorough study of the paired sense-organs found in the head of *Nereis virens*. I can, therefore, merely give the few facts of interest which have come under my observation during the foregoing study.

The two pairs of *eyes* have been described in *N. virens* by Andrews ('92) and I can add but little to this description. In some of my methylene blue preparations, the retinal cells were well stained and it could be distinctly seen that, in many cases, the peripheral protoplasmic ends of the retinal cells themselves passed through the pigment layer and appeared within the cup. The lens was shrunken and connected with the retinal rods by strands as described by Andrews. When the apex of a retinal cell appeared within the cup, it, too, was connected

with the lens by a delicate strand. According to Hesse ('99) the cells thus so connected with the lens are not visual cells but "Sekretzellen" by which the lens has been formed. In several eyes the striations always apparent in preserved lenses passed obliquely to the longitudinal axis of the lens and their arrangement strongly suggested the ovoid part of a spiral organ—the part formed by the enlarged ends of the peripheral processes, the refractive bodies, and the central tube—as seen in poorly preserved material. The structure and the probable function of these spiral organs and their position in line with the eyes, suggests the possibility that they represent the more primitive type from which the true eyes have developed. If the true eyes were derived from the spiral organs, or both are derived from the same more primitive organ, it is probable that the lens of the true eye is, as Andrews rather doubtfully suggests, actually composed of closely massed refractive bodies, each of which is but the transformed peripheral end of a retinal cell, and that the striations so often observed in preserved eyes are caused by the shrinking apart of the lens elements under the influence of reagents—a shrinking apart directly comparable to the separation of the component blocks of the spiral band in a spiral organ.

In *Nereis diversicolor*, Retzius ('95) was unable to find the optic nerves. In my preparations of *N. virens* it has been very easy to trace all four of these nerves from their respective eyes into the lateral surface of the brain and thence to its posterior part in which, according to Racovitza's ('96) investigations in *N. dumerili*, lie the four optic ganglia. The nerve fibers from the retinal cells are extremely delicate and in the methylene blue preparations each is always broken up into a row of minute, disconnected granules.

A number of very large unipolar ganglion cells are found beside each of the anterior eyes. The greater number of these cells are ventral to their eyes, but some are anterior and some lateral to them. A few of the cells extend so far peripherally among the epidermal cells as to almost touch the cuticula. Several of them lie in the main dorsal branch of the circum-

oesophageal commissure and some are found in this branch even after it has entered the brain itself. Each of these cells is plainly a ganglion cell and from each a single process can be seen passing into the main dorsal branch of the commissure just mentioned and then turning ventrad in this branch. I have not been able to trace the further course of these axis cylinders, but Hamaker ('98) states that they pass to the commissural ganglion and he apparently considers it possible that they are the ganglion cells which give rise to the "three giant fibers which traverse the ventral cord throughout its entire length." Each cell is itself enclosed in a fibrous capsule and its process or axis cylinder is surrounded by a large sheath which is a prolongation of this capsule. Retzius ('95) noted these ganglion cells in *N. diversicolor* and considered it possible that they were concerned with the innervation of the anterior eyes. Although Hamaker ('98) considered that this could not possibly be true, yet he has designated each of these groups of ganglion cells as an "optic ganglion." Such a designation is not only incorrect in itself since given to a ganglion having no connection with the eye except, in some species, the accidental one of position, but also leads to confusion since Racovitza ('96) has already designated as optic ganglia the regions in the posterior brain which receive the central fibers of the retinal cells.

The anterior paired cephalic organs are situated in the prostomium, one on either side, just at the angle which this part of the head makes with the palps (Plate I, Fig. 28). In a surface view of the prostomium taken from a worm injected with methylene blue, this organ appears as a deeply stained, ovoid body apparently formed of very coarse fibers whose peripheral ends branch in a twig-like manner just beneath the cuticula. Sections reveal the fact that this ovoid is really formed of very large bipolar cells which are mostly spindle-shaped (Plate I, Fig. 29). The central processes from each group of cells form a small nerve which passes directly to the anterior margin of the brain slightly mesad and ventrad of the palp nerve. This nerve now joins other nerves from the anterior part of the prostomium and the common nerve thus formed can be traced along the lateral

margin of the palp ganglion (see Text-figure 3). The peripheral processes from the cells of one of these organs usually branch several times. The ultimate ends of all of these branches come together in a small area just beneath the cuticula and each, as far as I have been able to make out, terminates in a little end-bush. The cell-bodies and peripheral processes of these organs lie in a large mass of fine, interwoven connective tissue. The dorsal part of this mass is cone-shaped and the apex of this cone appears to reach the cuticula and to contain the peripheral ends of the peripheral processes of one of these anterior organs. If this be correct, the peripheral processes of the cells in this organ would have no direct connection with epidermal cells or with the exterior. My sections, however, are not such as to enable me to decide this point with certainty. These organs were first seen by Retzius ('95) in *N. diversicolor*. He says concerning them: "Es findet sich in den Palpen, und zwar an ihrem inneren Umfange, jederseits ein eigenthümlicher Nerven- zweige welcher aus einer beschränkten Anzahl von Fasern besteht, die ein grob-variköses Aussehen darbieten und vorn einen kolbenförmigen Klumpen bilden. In diesem treten starke Verdickungen der Nervenfasern hervor, die jedoch nicht als kleine kernhaltige Nervenzellen imponiren, sondern eher das Aussehen von motorischen Nervenendigungen darbieten." An organ lies so close to a palp that a surface view would mislead one as to its position. My sections of *N. virens* plainly show that, in this species at least, this organ lies in the prostomium and also that the "starke Verdickungen der Nervenfasern" are nerve cells. It is evident that Retzius supposed these nerve-fibers to be motor fibers innervating the palps. The peripheral situation of the cells that give rise to these fibers, the appearance of the organs as a whole, and the fact that the peripheral processes appear wholly unconnected with muscles, would all tend to prove that this is a true sense-organ. Of its probable function I can at present only conjecture.

I have several times seen an appearance that suggests that the surface of the palp adjacent to the organ just described is modified into some sensory structure. In the base of the epi-

dermis of a small area are a number of apparently isolated, spindle-shaped, bipolar nerve-cells. The peripheral process of each cell appears to pass in a small canal through the cuticula and to project above the surface as a sensory hair. The central processes from these cells join each other to form small nerves which later unite and pass to the brain. If this observation should be verified, there would be proved to be on the base of the inner side of each palp a small sensory area thickly covered with cilia which are born by nerve cells apparently identically like the component cells of the diffuse sense-organs.

Each of the *posterior pair of cephalic organs* lies on the anterior surface of a little pocket-like invagination which is situated between the prostomium and peristome just caudo-laterad and somewhat ventrad of the posterior eyes (Plate II, Fig. 28). Retzius ('95) has briefly described these organs in *Nereis diversicolor*; Racovitza ('96) has made a somewhat extended study of them—he calls them “*Organe nucae*”—in *Nereis dumerili* and in many other Polychætes. Hamaker ('98) has given a partial description of them in *N. virens* itself. These organs in *Nereis virens* are practically the same as those described for the two species studied by Racovitza. Each is an elongated area of very long epidermal cells among whose peripheral ends lie the free terminations of the peripheral processes from a group of bipolar nerve-cells situated in the posterior brain. I have, however, found among the central ends of the epidermal cells of this area the wandering cells bearing yellow pigment which Racovitza has described in other genera but not in *Nereis*. I have not been able to see that the final ends of the central fibers from the nerve-cells end in fine branches as described by Retzius nor that the epidermal cells bear cilia as described by Racovitza and Hamaker. My failure to observe the latter is, I am sure, due to my material, not to the absence of these cilia. Racovitza states that these organs are difficult to see in the living animal because “ils sont cachés sous un repli du bord antérieur du premier segment,” a view also held by Hamaker. It is, however, more than these folds which conceals these organs. Each is really situated on the anterior surface of a pocket-

like invagination—an invagination which is easily seen in the removed cuticula. To the cuticula in the base of each invagination is attached a large muscle which is probably one of the muscles of the proboscis, and it is, I believe, the pull of these muscles which has caused these invaginations: the two posterior sensory organs have come to lie in these pockets through the accident of their position. It appears to be generally true in *Nereis* that muscles are often attached to the cuticula and that such lines of attachments become the bases of grooves. These posterior cephalic organs have been supposed by different writers to serve every special sense except that of sight. Racovitza ('96) concludes that they are olfactory organs. Their structure, position, and innervation correspond to the so-called olfactory organs of other worms in which undoubted otocysts are also present (see Gamble and Ashworth's account of *Arenicola marina*); but the presence in *Nereis virens* of one and possibly two other pairs of cephalic organs of unknown function renders necessary an extended study of the latter before the function of any of them can be absolutely decided for this worm. In any case the presence of a sensory area in an invagination which is apparently due to muscular action gives a very suggestive theoretical explanation of the primary cause of such invaginations as are found in some otocysts—invaginations which merely serve to increase the sensory epithelium in higher animals in which the proboscis has disappeared.

VII. *Epidermal Anchoring Cells.*

I have given this name to certain epidermal cells which seem to be intimately connected by one end with the cuticula and by the opposite end with muscle fibers passing to the epidermis. Each of these cells, when stained by methylene blue, is seen to have a very slender somewhat cylindrical or prismatic body, one, two, or three diverging basal processes, and a large number of peripheral processes. (Plate II, Fig. 49). The body of an anchoring cell extends from the cuticula centrally about to the middle height of the epidermis and contains a more deeply stained oval nucleus at or beneath the middle of

its height. Above its nucleus, each cell-body is of almost uniform width; below, it tapers to its central end. The part of the cell which touches the cuticula is always deeply stained and enlarged. This enlargement has the appearance of a varicosity and from it a number of fine strands run into the cuticula just above, passing almost or quite through the inner layer of the latter. At first sight these strands appear like sensory hairs but a comparison of their appearance with that usually presented by a sensory hair reveals several important points of difference. Each sensory hair lies in a special canal of its own whose outline, in some cases at least, can be clearly distinguished. Some of the sensory hairs are always found passing through to the exterior in methylene blue preparations. Some are irregularly varicose and some are always stained continuously for their whole length; when one is broken up into small separate parts, these parts are always rounded. I have never found a peripheral process from one of these anchoring cells stained continuously or presenting any varicosities—each process is evenly broken up into minute cylinders placed end to end; I have never found one of these processes passing through the cuticula to the exterior—they all lie in the inner cuticular layer; neither have I found any trace of a special canal around any of these process—each seems to be simply inclosed in and almost a part of the cuticula. The appearance presented by a group of these processes suggests that delicate strands have grown out into the cuticula from the apex of each anchoring cell and have become intimately connected with the latter and that, under the influence of reagents, a decided contraction had taken place. Then, because the peripheral processes were too intimately connected with the inner layer of the cuticula to become wholly withdrawn beneath the latter, some of the protoplasm in the apex of the cell, and perhaps a little from the very base of the peripheral processes, became gathered into the varicosity usually found just beneath the cuticula and the processes themselves became broken up into tiny cylinders.

If the outer layer of the cuticula is shed, these protoplasmic strands must either constantly grow from the apex of their cells

at the same rate as the cuticular layer grows by addition to its inner surface, or else the strands must shift their attachment. The former appears the more probable at present but it can only be decided by further study.

The basal processes from these anchoring cells are never beaded or varicose as are the central processes from the nerve-cells. Over the surface of each one can always perceive either a single row or two parallel rows of small blue cylinders like those of the peripheral processes only slightly larger. This appearance I have never seen in a nerve-fiber of *Nereis virens* but have often found on the surface of a muscle-fiber. The fact that these broken cylinders, instead of the varicosities usual in nerve tissue, are found in the central processes which are free from other structures except at their ends, shows that their form can not be due to the processes being firmly embedded in a surrounding tissue, as one might suppose from a study simply of the peripheral processes, but must be due to some intrinsic difference in the tissues themselves. These basal processes can be traced directly past the nerves in the base of the epidermis *to the peripheral end of one of the muscles which pass in large large numbers to the epidermis.* Sometimes these processes appear to enter the muscle itself and sometimes to pass onto its outer surface. It would, therefore, appear that *these anchoring cells serve for the attachment of muscles to the cuticula.* The peripheral strands embedded in the cuticula anchor the cells at their peripheral ends; the basal processes are either interwoven with the connective tissue at the peripheral end of the muscle or else actually form this tissue itself, thus forming a sort of muscle tendon.

It will be remembered that a number of rather large pores were found in the cuticula around the perforated membranes belonging to the diffuse sense-organs in the tentacles and the tips of the palps. (See Plate I, Fig. 8). In the palps many small muscles pass toward the cuticula among the bodies of the epidermal cells. It seems to me probable that these muscles are attached to the cuticula by just such anchoring cells as are described above and that this attachment is strong

enough to tear an opening entirely through the cuticula when the latter is removed. Since the cuticula in the palps is much thinner than that over the body it may be that the peripheral processes of the anchoring cells in the former region extend entirely through the inner cuticular layer, into the outer layer, or it may be that there is a more intimate connection between the two layers of cuticula themselves than between those of the the body. Either supposition would account for the fact that these openings are so often found in these two appendages and so rarely in the body. As only a very few anchoring cells were stained in the palps, I was not able to decide this question by actual study. In the tentacles there are no muscles, but a number of very coarse connective tissue strands pass from the base of the tentacles toward the cuticula and these strands may be basal processes of anchoring cells, processes connected with muscles at the base of the tentacles. When the cuticula is removed from the ventral surface of *Nereis*, there is sometimes found in it large circular openings in those places to which the ventral oblique muscles pass; these openings, it seems to me, are also due to the firm attachment of groups of anchoring cells.

I have been able to examine only the head and first metamere for these anchoring cells. In these regions, they are present in the epidermis wherever muscle-fibers pass to or into the latter. They are especially numerous in the epidermis of the grooves which pass across the prostomium and to which large numbers of muscle-fibers are attached. I have found them at the bases of the cephalic appendages, at the insertion of the muscles moving these appendages, and at the point of insertion of the ventral oblique muscles of the first metamere.

I have found no description of cells exactly like these anchoring cells of *Nereis* but I have found two references to epidermal cells which may be, I think, such cells. Andrews ('92) after describing the apparent connection of the retinal cells in the eye of *Eunice* with the lens itself states that: "Some views of the common epidermis of the head lead one to infer that here also the attenuated cells amongst the larger epidermal cells have a close connection with the cuticula like

that of the above cells with the lens." Zernecke ('95) has figured and described in the subcuticular region of Ligula cells from whose narrowed peripheral ends a number of fine processes pass into the cuticula without any definite canals and sometimes, though not always, end under an insinking from the exterior; from the basal end of each cell one or two processes are given off which never appear to be connected with nerves. Zernecke calls these cells "Korbchen-zellen" and says they "stehen vielleicht im Dienste der Nahrungsaufahme." It seems to me not impossible that both the "attenuated cells" of Eunice and the "Korbchenzellen" of Ligula may be anchoring cells for the attachment of muscles to the cuticula. If this proves true, the insinking sometimes seen in the cuticula of Ligula over one of these cells, will probably be found to be due to a contraction of these cells and their muscles—a contraction due to the influence of reagents and strong enough to tear the peripheral processes of the cells and the cuticula to which they are attached away from the surrounding cuticula.

SUMMARY.

I. The Diffuse Sense-Organs.

1. The epidermis of *Nereis virens* contains a peripheral sensory system composed of bipolar nerve-cells, which, except for some doubtful cases in the parapodial cirri, are always grouped into definite sense-organs.

2. The bodies of the cells in these sense-organs, in all regions of the body, are always situated in the epidermis itself.

3. From the peripheral end of each sense-organ a bundle of nerve-fibers—the peripheral processes of the nerve-cells—passes to the cuticula and into a differentiated area in the latter—an area composed of a deep inner and a shallow outer cavity separated by a perforated membrane of cuticula. In the inner cuticular cavity some of the peripheral processes branch. Each finally terminates in a sensory hair. All of the sense-hairs from a single organ pass to the exterior by means of the canals in the perforated membrane belonging to the organ in question and are, therefore, in direct communication with the external world.

4. From the central end of each organ, a second bundle of nerve-fibers—the central processes of the nerve-cells—passes into the central nervous system or into peripheral ganglia connected with the latter and seem to form pericellular nerve-baskets around the ganglion cells there present.

5. The diffuse sense-organs are most numerous in those regions of the body that are most exposed to contact.

6. It is probable that these organs serve for the perception of chemical and mechanical stimuli. Similar organs which exist in the epithelium lining the buccal cavity probably serve as gustatory organs.

II. The Spiral Organs.

1. The epidermis of the gill-lobes, of the enlarged bases of the palps and cephalic cirri, and of about the first twenty metameres of *Nereis virens* contains complicated organs which probably form a second system of sense organs.

2. Each of these spiral organs consist of about 100 bi- or multipolar cells—apparently nerve-cells—whose peripheral processes are arranged spirally around a central tube—a tube apparently formed of invaginated cuticula.

3. The bodies of the cells composing the spiral organs lie in the base of the epidermis or in special pouches which project centrally from this base.

4. The peripheral processes are club-shaped and the tip of each contains a refractive body. The terminal halves of these refractive bodies are so arranged as to form a spiral band around the central tube.

5. The central processes have been traced only a short distance centrally; it can be seen that they pass toward and almost into the epidermal nerves.

6. The spiral organs are most numerous on those portions of the body which are likely to be most directly exposed to the light.

7. They resemble the epidermal eyes of Invertebrates and some of the simpler true eyes of the Polychætes; their function is probably the perception of difference in intensity of light.

III. The Paired Cephalic Organs.

1. The prostomium contains four pairs of special sense-organs, two pairs of eyes in its dorsal surface, one pair of problematical organs in its anterior margin, and a second pair in its posterior margin. There also appears to be present near the base of the inner side of each palp a ciliated area which may prove to be a second pair of anterior cephalic organs.

2. The evidence at hand goes to prove that the true eyes are derived either from the spiral organs themselves or some more primitive type common to both. It also supports Andrews' suggestion that the lens in the true eyes is composed of the transformed tips of the retinal cells—the "Sekretzellen" of Hesse.

3. The anterior pair of cephalic organs are each composed of a group of large bipolar nerve-cells whose peripheral processes branch and finally terminate in end-brushes just beneath the cuticula, apparently without any connection with epidermal cells, and whose central processes pass into the brain.

4. The posterior pair are also each formed of a group of bipolar cells, but these cells have their bodies situated in the brain itself and their peripheral processes terminate among special epidermal cells which lie on the anterior face of two invaginations. These invaginations appear to be due to the pull of large muscles—not to the necessities of the sense-organs contained in them.

IV. The Epidermal Anchoring Cells.

1. There are also found among the common epidermal cells of *Nereis virens* modified epidermal cells which I have called anchoring cells.

2. The body of one of these cells does not appear to differ from the bodies of the supporting cells of the epidermis.

3. From the peripheral end of each anchoring cell a large number of fine processes pass into and are firmly embedded in the inner layer of the cuticula just above the cell.

4. From the basal end of each cell a small number of slender processes pass to or into the latter.

5. These anchoring cells apparently serve for the attachment of muscles to the cuticula.

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DESCRIPTION OF PLATES.

Figs. 2-4, 12, 13A, 13B, 18-20, 22-27, 33, 35, 36, 38, 42, 43, 47 and 48 are free-hand drawings made from material studied under the 2 mm. oil immersion objective and compensating oculars 8-12. Except where noted, all the other figures were made from camera outlines and filled in with the 2 mm. oil immersion obj. and comp. os. 8-12.

REFERENCE LETTERS.

a—area of attachment of anchoring cells *c. s.*—sensory cell.

ax. cy.—axis cylinder.

b. r.—refractive body.

bl. v.—blood-vessel.

c. anch.—anchoring cell.

c. ep.—epidermal supporting cell.

c. g.—ganglion cell.

c. gl.—gland cell.

cap. g.—capsule of ganglion cell.

can. cu.—cuticular canal of spiral organ.

cav. cu¹.—outer cuticular cavity.

cav. cu².—inner cuticular cavity.

cav. ep.—epidermal cavity in tactile appendage.

cir.—cirrus.

<i>cu.</i> —cuticula.	<i>o. ceph. p.</i> —posterior cephalic organ.
<i>cu</i> ¹ .—outer layer of cuticula.	<i>or. s.</i> —diffuse sense-organs.
<i>cu</i> ² .—inner layer of cuticula.	<i>or. sp.</i> —special organ.
<i>cu. a.</i> —modified cuticular area.	<i>pal.</i> —palp.
<i>e.</i> —eye.	<i>par.</i> —parapodium.
<i>f. nv.</i> —nerve-fiber.	<i>pers.</i> —peristome.
<i>f. s.</i> —sensory fiber.	<i>pig.</i> —pigment granules.
<i>gr. inter.</i> —intersegmental groove.	<i>pr. bas.</i> —basal process.
<i>h. s.</i> —sensory hair.	<i>pr. cen.</i> —central process.
<i>m. bas.</i> —basement membrane.	<i>pr. per.</i> —peripheral process.
<i>m. cu.</i> —perforated cuticular membrane.	<i>pros.</i> —prostomium.
<i>met.</i> —metamere.	<i>p.s.</i> —sensory pore.
<i>n.</i> —nucleus.	<i>t. cen.</i> —central tube.
<i>nv.</i> —nerve.	<i>ten.</i> —tentacle.
<i>o. ceph. a.</i> —anterior cephalic organ.	

DESCRIPTION OF PLATE I.

The drawings were made in ink and were reduced slightly more than one-half linear in the plate.

Fig. 1. The diffuse sense-organs in a cephalic cirrus as shown in a longitudinal section. Only the organs on one side of the axial nerve are shown. The base of the cirrus is toward the left. From a methylene blue section restained by alum cochineal. (The outlines were made with the Zeiss projection apparatus, obj. 35 mm., no ocular).

Fig. 2. Two diffuse sense-organs whose cell-bodies lie in one group. From an optical section of a living, unstained cephalic cirrus.

Fig. 3. Epidermal cavity and normal sense-hairs of a diffuse sense-organ in a cephalic cirrus. From an optical section of living, unstained material.

Fig. 4. Epidermal cavity and abnormal sense-hairs and peripheral processes of a diffuse sense-organ in a cephalic cirrus. An optical section from dying material injected with methylene blue.

Fig. 5A. A longitudinal section of the modified cuticular area of a diffuse sense-organ in a cephalic cirrus. From a methylene blue section restained by alum cochineal.

Fig. 5B. A longitudinal section of the modified cuticular area and peripheral processes from a diffuse sense-organ in a ventral parapodial cirrus. From a methylene blue section restained by alum cochineal.

Fig. 6. A surface view of the modified cuticular area belonging to a diffuse sense-organ in the cephalic cirri. From a surface view of the removed cuticula.

Fig. 7. A longitudinal section through the base of a dorsal parapodial cirrus showing *apparently* isolated sense-cells. From a methylene blue section restained by alum cochineal. A sense-cell which was unstained by the blue is shown at the right.

Fig. 8. A surface view of the modified cuticular area of a diffuse sense organ in retractile tips of the palps. From a surface view of the removed cuticula.

Fig. 9. A longitudinal section of the modified cuticular area of a diffuse sense-organ in the peristome. The portions of the peripheral processes in

the inner cuticular cavity and the sense-hairs appear to be nearly normal. From material killed in Müller's fluid and stained with Kleinenberg's hæmatoxylin.

Fig. 10. Omitted from the plate.

Fig. 11. A surface view of the modified cuticular area of a diffuse sense-organ in the body epidermis. From a surface view of the removed cuticula.

Fig. 12. Normal shape of the bodies of the sense-cells of the diffuse sense-organs in the cephalic cirri. From living unstained material.

Figs. 13 A and B. Two optical longitudinal sections of the epidermal cavities of the diffuse sense-organs in the cephalic cirri. From living, unstained material. In *Fig. 13 B* the position of the peripheral processes of an epidermal cavity is shown.

Fig. 14. A longitudinal section of a diffuse sense-organ in the tentacles. From methylene blue material restained by alum cochineal.

Fig. 15. A longitudinal section of a diffuse sense-organ in the palps. From methylene blue material restained by alum cochineal.

Fig. 16. A longitudinal section through the modified cuticular area of a diffuse sense-organ in the cephalic cirri. From methylene blue material restained by alum cochineal.

Fig. 17. A longitudinal section of a diffuse sense-organ in the base of the dorsal border of a dorsal parapodial cirrus. From material killed in alcohol and stained with Kleinenberg's hæmatoxylin.

Fig. 18. The outline of a longitudinal optical section of a dorsal parapodial cirrus showing the arrangement of the sense-hairs in definite groups along the dorsal and ventral borders and the apparently isolated ones at the tip of the cirrus. From living, unstained material.

Fig. 19. The surface view of one-half the surface of the distal part of a cephalic cirrus. The location of the modified cuticular areas of the diffuse sense-organs is marked by the circles over the surface and by the groups of sense-hairs around the margin. The tip of the cirrus was so transparent that the location of the sense-organs in it could not be seen. From living, stained material.

Fig. 20. A group of sense-hairs which have become swollen into balls resting on the cuticula. From a diffuse sense-organ in unstained dying material.

Fig. 21. A surface view of one side of a dorsal parapodial cirrus. The distribution of the modified cuticular areas of the diffuse sense-organs in the surface is shown by the circles. The sense-hairs around the margin did not show (see *Fig. 18*). A camera drawing from living stained material.

Fig. 22. A few of the cells of a spiral organ in a gill-lobe. From an optical view of living material that had been injected with methylene blue. In this organ only the cells shown in the figure took the blue.

Fig. 23. The sense-hairs of the diffuse sense-organs along the dorsal border of a dorsal parapodial cirrus. The hairs near the base appear to be isolated, those nearer the tip appear to be arranged in groups. The base of the cirrus is toward the left. From living unstained material.

Fig. 24. Sense-hairs in diffuse sense-organs from a parapodial cirrus. Each hair has its tip swollen into a little ball. From dying unstained material.

Fig. 25. A sense-hair which has become thickened at its base. From a diffuse sense-organ in a dying parapodial cirrus.

Fig. 26. Four views of a single sense-hair of a diffuse sense-organ showing successive stages in the withdrawal of a hair which has its apex already swollen into a ball. From a dying parapodial cirrus.

Fig. 27. The normal sense-hairs of three diffuse sense-organs situated in the dorsal border of a dorsal parapodial cirrus. From living, unstained material.

Fig. 28. A diagram showing the distribution of the spiral organs as far back as the first metamere. A wax model was constructed from sections and the position of each spiral organ marked on the surface. Tissue paper was then carefully fitted over the surface of the left half of the model and the position of each organ, as seen through the tissue paper, was marked in pencil on the latter. The tissue paper was then straightened and the chart thus obtained transferred to drawing paper. The right hand margin of the figure represents the mid-dorsal line and the left one the mid-ventral line. The position of the spiral organs is shown by the black dots. The broken lines mark the position of grooves in the surface.

Fig. 29. The cell-bodies and a few of the peripheral processes of one of the anterior cephalic organs as seen in a longitudinal section of the prostomium. From methylene blue material restained by alum cochineal.

DESCRIPTION OF PLATE II.

Figs. 30-32. Longitudinal sections of diffuse sense-organs in the peristome. The sensory hairs were mostly withdrawn. Fig. 30 shows the connection of a central process with an epidermal nerve and Fig. 32 shows an organ in which but one of the nerve cells has taken the blue. From methylene blue material restained with alum cochineal.

Fig. 33. Optical view of a diffuse sense-organ in a cephalic cirrus. The under side of the perforated membrane is shown. From living, methylene blue material.

Fig. 34. A longitudinal section of the modified cuticular cavity of a diffuse sense-organ in the peristome. One sense-hair retains its normal position. The rest have been withdrawn into the inner cuticular cavity. From methylene blue material restained by alum cochineal.

Fig. 35. A single nerve cell belonging to a diffuse sense-organ in the cephalic cirri. The peripheral process of this cell has four branches. Varicosities have formed at the tips of the sensory hairs and one large one in the peripheral process itself. From dying, methylene blue material.

Fig. 36. An optical longitudinal section through the tip of a cephalic cirrus. The sense-hairs belonging to two diffuse sense-organs are shown and one peripheral process which took the blue and which has a large varicosity. From dying, methylene blue material.

Fig. 37. An oblique section of a modified cuticular area of a diffuse sense-organ. The outer cuticular cavity does not appear in this section. One peripheral process branches in the inner cuticular cavity. From methylene blue material restained by alum cochineal.

Fig. 38. Optical view of the peripheral processes of the diffuse sense-organs whose cells lie in a single group. The perforated membranes are shown from underneath. From a living cephalic cirrus stained by methylene blue.

Figs. 39 and 40. Apparent pericellular nerve-baskets around ganglion cells in a cirrus ganglion. Fig. 39 shows the position of this basket in relation to both the ganglion cell and its capsule. The protoplasm of the cell has shrunk. Fig. 40 shows the centripetal nerve-fiber around the axis-cylinder of the ganglion cell. From sections of methylene blue material restained by alum cochineal.

Fig. 41. A longitudinal section of a spiral organ in the peristome. From material killed in Müller's fluid and stained with Kleinenberg's hæmatoxylin.

Figs. 42 and 43. Optical sections of parts of two spiral organs in the gill lobes. In Fig. 43 the whole of the central tube and a surface view of its external opening is shown. Fig. 42 shows the base of an organ. From living, unstained material.

Figs. 44 and 45. Two abnormal appearances sometimes seen in longitudinal sections of the outer ends of spiral organs, appearance apparently due to the central tube contracting away from the surrounding cuticula. From material killed in Müller's fluid and stained with Kleinenberg's hæmatoxylin.

Fig. 46. A lateral view of a tip of one of the peripheral processes belonging to a spiral organ. In this tip only the apical block of the refractive body could be seen (see Text-figure 4). From material killed with alcohol and stained with Kleinenberg's hæmatoxylin.

Fig. 47. An optical section of the summit of a spiral organ showing the apical turn of the spirally arranged peripheral processes. The cuticula is shown in surface view. From living, unstained gill lobes.

Fig. 48. Several peripheral processes containing abnormal or accessory refractive bodies. From spiral organs in living, unstained gill lobes.

Fig. 49. Two of the epidermal anchoring cells as seen in a longitudinal view of the peristome. From methylene blue material restained with alum cochineal.

DESCRIPTION OF PLATE III.

This chart was made from the removed cuticula by means of the Zeiss projection apparatus fitted with obj. 35 mm. and no eye piece. It was drawn to a scale of 1 dm. for 2 mm. and has been much reduced in the plate.

Fig. 50. A chart showing the distribution of the diffuse sense-organs. This chart is from one half the cuticula extending from the mid-dorsal line to the mid-ventral line. The metameres are separated by heavy black lines which represent the intersegmental grooves; other grooves are shown by broken lines. The small black dots represent the cuticular areas over the sense-organs.

Fig. 51. The arrangement of the modified cuticular areas belonging to the diffuse sense-organs as shown in a bit of the cuticula from near the base of a cirrus (compare with Fig. 19).

FANNY E. LANGDON.

While this paper was passing through the press Miss Langdon died (Oct. 21, 1899) after a brief illness following an operation for appendicitis.

She was born at Plymouth, N. H., in 1865, and received her early education in the public schools of the village and in the State Normal School of New Hampshire. She then taught for several years in the primary schools of the state, and in 1891 entered the University of Michigan where she began at once to specialize in botany and zoölogy. She received the bachelors' degree in 1895 and masters' degree in 1896. In the summer of 1897 she was a student at the Wood's Hole laboratory. She was for two years (1895-7) assistant, and for one year (1897-8) instructor in the botanical department of the University of Michigan. In the fall of 1898 she became instructor in zoölogy in the same university and held the position at the time of her death.

In 1895, while an undergraduate, she published in the *Journal of Morphology* a paper on "The Sense Organs of *Lumbricus agricola* Hoffm." At the time of her death she had nearly completed an important botanical paper "On the Development of the Flowers of the Asclepiadaceæ." She had expected to finish this paper during the present academic year and afterward to give her whole attention to zoölogy. From the many notes, drawings and specimens that she has left it is hoped that it may be still possible to prepare the paper for the press.

Miss Langdon was never robust, and her scientific career was a heroic and inspiring struggle against ill health. She began the work of the present year with health apparently quite restored and, until the end came, her friends were hopeful that she had before her a long career of scientific usefulness.

That she stood high as an investigator is known to many readers of this journal, who have recognized the painstaking conscientiousness and accuracy of her observations, and the alertness and acumen of her discussions. She was an inspiring laboratory teacher and a clear and forcible lecturer. Those personal characteristics that endeared her to her friends and have moulded her scientific work were, besides a marked ability, conscientiousness and fealty. All her work was her best work. It was well done, not in her interest solely, but for its own sake.

JACOB REIGHARD.

THE ROOF AND LATERAL RECESSES OF THE FOURTH VENTRICLE, CONSIDERED MORPHO- LOGICALLY AND EMBRYOLOGICALLY.

By JOSEPH A. BLAKE, M.D.

[Read before the Association of American Anatomists, Eleventh Annual Session, New York, Dec. 28, 1898.]

My investigations on this subject were prompted by the contradictory opinions and the lack of absolute knowledge concerning the nature of the communications between the cavity of the fourth ventricle and the subarachnoid space.

At first my efforts were confined to the study of the morphology of the metapore, or foramen of Magendie, but I soon found that it was necessary to include that of the entire roof of the ventricle, and then naturally followed an elucidation of the problems found in the lateral recesses.

The development of the roof of the ventricle is very closely connected, it is needless to say, with that of the oblongata and cerebellum.

The development of the oblongata in man has been worked out by His, but we need further knowledge of its development in the lower animals. Our knowledge concerning the cerebellum is as yet unsatisfactory.

The lateral recesses have been ably described by Mihalco-vics and by Retzius, but the descriptions in our text-books are, as a rule, faulty, if not incorrect.

Their relations to the medulla and cerebellum and their segmental value have not been sufficiently determined.

Hitherto the investigations on the metapore and foramina of Luschka have been chiefly to determine their presence, while their nature has been largely a matter of supposition. The methods employed have been almost entirely those of in-

jection and of inspection by careful dissection or gross sectioning.

A brief résumé of the results of these investigations is as follows: Key and Retzius found the metapore present in 98 out of 100 cases examined. In one of the exceptions there was a continuous tela. They also found the lateral recesses open in all but three. In two brains it was closed on both sides and in one brain on one side. C. Hess examined the brains of 30 adults, 10 new-born children and 7 embryos of different stages, and found the metapore absent in one. In 54 lateral recesses he found all open except two. Others who do not give the number of brains investigated and who found the metapore present are, Wilder, Morton, Kohlmann, Jacobi and others, and its presence is conceded in most of the descriptive anatomies.

On the other hand, Kölliker states that the cavity is originally closed and always remains so, and Reichert that both the metapore and foramina of Luschka are artifacts. Its presence is questioned by Cruveilhier and See. The openings in the lateral recesses, first discovered by Luschka, have been most fully described by Key and Retzius, and later by Retzius, by Hess and by Mihalkovics. Their presence is doubted by Wilder.

In the lower animals most observers agree that the metapore is absent but that the lateral recesses are open. Wilder has found the metapore in the chimpanzee, baboon and several old world monkeys. Hess found openings in the roof of the ventricle of an embryo cat. Jacobi has proved the presence of openings of the lateral recesses in the live dog by injecting methyl blue into the subarachnoid cavity in the lumbar region and having it emerge from a cannula placed in the ventricle of the brain and vice versa.

In the last year articles on the metapore and the foramina of Luschka have appeared by A. Cannieu. His investigations were partially by gross methods and partially histological. By gross methods he found the metapore present in the dog, cat, rabbit, guinea-pig, horse, ox, ass, and in man. He allowed the brains of the lower animals to soften so that they would approximate the condition in which it is usual to obtain human

brains. By histological methods he found it absent in the dog and cat, and concluded that its apparent presence in all animals is due to a poor state of preservation of the brain. Also by histological methods he finds that the lateral recesses are closed in the lower animals.

In regard to the appearance of the metapore, we find that the usual description is that it is a perforation in the roof of ventricle at the region of the calamus, varying in size and with more or less ragged edges.

Henle, Schwalbe and Key and Retzius describe its margins as smooth or rounded, and the latter give its dimensions and boundaries. Hoffman and Rauber describe it as appearing like a short tube and not as a break in a membrane.

C. S. Minot has suggested that it might be the orifice of an evagination of the endyma. But as to whether he thinks the orifice normal or artificial is not stated.

The condition of these openings found in pathological states of the brain vesicles, as hydrocephalus, cysts, etc., is of interest as bearing upon their function and their necessity. The evidence thus obtained, it must be confessed, is fragmental and inconclusive largely on account of the lax methods and observations employed in autopsies.

Absence of the metapore has been reported by O'Carroll in two cases of hydrocephalus, by Neurath in another, and A. Henle attributes hydrocephalus largely to the closure of the ventricular openings. Sutton states that early closure gives rise to ventriculo-meningocele and later closure to localized cysts.

Hydrocephalus is also attributed to the presence of tumors, especially in the regions of the mid- or hind-brain.

Magendie has reported two cases of closure and concomitant hydrocephalus in old people; Martin St. Ange one in an 8-year old child; Virchow a case of closure of lateral recesses with localized cysts. The metapore has been reported open by Morton in seven cases of tubercular meningitis, even where the pia was much thickened. The efficacy of lumbar puncture in hydrocephalus is admitted by many (A. Broca, P. Maudslayi, Quincke, Jacobi), and Quincke has withdrawn 100 cc. of

fluid in one sitting by this method from a case of hydrocephalus due to a tumor, an amount which could hardly have been afforded by the spinal subarachnoid space with its unyielding walls.

The evidence in regard to the function of the communications is more or less negative in these cases, for a hydrocephalus might occur with the openings present and be due to a fault in the absorbents.

But the more numerous the cases of hydrocephalus with closure of the communications, with otherwise normal condition of the structures, the stronger the evidence that they are functional in allowing the passage of the cerebro-spinal fluid.

The present contribution is based upon researches conducted for the greater part microscopically upon both adult and embryonic brains, both of man and the lower mammals. All the objects were cut serially; great difficulties were encountered from the necessity of keeping the membranes intact.

In so far as practicable the entire head was cut; when this was impracticable, either a portion of the head containing the cerebellum and oblongata with the tentorium intact was decalcified and sectioned, or the entire brain was hardened in situ, generally by the intra-arterial injection of formalin, and the cerebellum and oblongata with their surrounding membranes then carefully isolated by cutting away the adjacent structures.

The reagents used for fixation and hardening were generally formalin or a mixture of formalin and bichromate of potash; other usual fixatives were also employed for the embryonic material.

Both celloidin and paraffin were used for embedding, chiefly the latter.

The most valuable stain for adult forms was found to be Van Gieson's, it giving a very clear differentiation between the membranes and epithelium. The usual hæmatoxylin and carmine stains were used for the embryonic material with combination stains.

In the illustration of this paper I am indebted to Mr. E. A. Spitzka who made all the drawings of sections.

NOMENCLATURE.

Inasmuch as there are some apparent inconsistencies in the nomenclature employed, it is well to call attention to them, so that they will not be misunderstood.

As generally accepted, the third cerebral vesicle is divided into two encephalic segments, the epencephal and metencephal, the corresponding cavities being the epicœle and metacœle.

These terms have been used in several of the accompanying drawings, and also the term fourth ventricle—Figs. 12, 13 and 14, for example.

The writer is unable to accept, for reasons that will appear later, the division of this part of the brain into two segments, and has used the terms metacœle and epicœle to emphasize the fact that they cannot be made to apply to a considerable portion of the fourth ventricle.

Objection may be made to the use of secondary rhomboidal lip in figures of advanced embryos and adults, when that structure no longer exists as such. The reason for its employment in these cases is to indicate the derivation of the structure thus designated, its adult name being also added when it seemed necessary.

In order to fully comprehend the conditions found in the adult fourth ventricle, it is necessary to follow the development from early embryonic stages, i. e., before the institution of the pons flexure.

The roof at this period is comparatively simple, but soon complications appear, due to change in the margins of the ventricle or rhomboidal fossæ, as it is generally termed.

Later the involution of vessels to form the choroid plexus appears, together with the pons flexure.

Thus it is convenient to classify the study of the roof as follows :

- I. The line of attachment of the roof.
- II. The choroidal fold.
- III. The roof as a whole.

LINE OF ATTACHMENT OF ROOF.

The attachment of the roof is largely influenced by the changes which take place in the margins of the rhomboidal fossa.

As has been shown by His, the neural tube is divided into four longitudinal laminæ, two dorsal and two ventral (Flügelplatte and Grundplatte).

These laminæ are well marked in the spinal cord and medulla at early stages. The two dorsal laminæ are connected by the roof plate and the ventral laminæ by the floor plate.

The oblongata is characterized by the separation of the dorsal laminæ and consequent widening of the roof plate. Fig. 1.

This separation begins at the calamus region and is most marked at this region of the auditory vesicle and the interval then decreases rapidly and the laminæ meet again caudad to the isthmus where they form the proton or fundament of the cerebellum (His).

In human embryos of the fifth week, ten millimeters long, according to His, a marked folding of the dorsal margins of the dorsal laminæ occurs.

This takes place throughout the whole length of the rhomboidal fossæ and the attachment of the roof is thus further shifted laterad. In a few days this fold fuses to the outer surface of the dorsal laminæ, at the same time its margin of attachment to the roof becomes drawn out into another fold or lip which tapers into the epithelium of the roof. His calls the first fold the Rautenlippe and the second the secondary Rautenlippe; as anglicized by Minot the rhomboidal lip and the secondary rhomboidal lip. Fig. 1.

Hitherto the primary rhomboidal lip has not been demonstrated in the lower mammalia.

Evidences of it appear in several rather advanced embryos I have studied, namely, in the pig, sheep, cat and rat, as a rounding of the dorsal margin of the dorsal lamina and an apparent shifting of the roof attachment which does not proceed

so far as to form a lip but gives rise to what simulates the Flügelwülste of His, i. e., the rounding formed by the growth of the rhomboidal lip.

Its existence in rabbit embryos has been denied by Dexter.

Lately¹ I have been able to demonstrate conclusively its existence in the rat embryo of three millimeters N. B. length. Fig. 1.

Its development does not proceed so far in the lower mammals as in man, especially in the region of the cerebellum. It certainly does not achieve the morphological importance attributed to the rhomboidal lip by His in man, namely, the covering in of the funiculus solitarius and the formation of the raphé and olive, unless we can consider this process to take place by an emigration of the neuroblasts from the lip rather than by an actual folding of the lip around the medulla, which latter seems to me an unsubstantiable proposition.

The existence of a primary rhomboidal lip in a non-fused condition in the lower animals, is probably extremely transitory, which explains its hitherto apparent absence. With the formation and fusion of the rhomboidal lip the secondary rhomboidal lip makes its appearance.

The secondary lip is essentially a transition between the nervous parietes and the roof and it partakes in its constitution of the characters of both. It commences as a lamina of nervous matter and thins away more or less quickly into the roof.

In man it reaches its greatest development, but it was present in all the embryos and adult animals studied.

The primary rhomboidal lip is narrow in the calamus region and then broadens somewhat in the region of greatest width, but reaches its greatest extent in the cerebellar region. Figs. 5, 6, and 8.

His states that in the calamus region it later becomes separated from the sides of the oblongata, but I am inclined to think that what appears as a separation is really the development of the secondary lip. In any case in this region the dis-

¹ Within a few weeks after the reading of this paper.

inction between the two is not marked and is rather one of degree than of absolute limitation.

In my descriptions I designate the portion giving direct origin to the roof plate as the secondary lip and reserve the primary lip for the bending of the substance of the dorsal lamina.

The directions of the two lips are different as a rule, but in the region of the lateral recess they coincide and it is impossible to make a definite separation of them in later stages. Figs. 4, 8, 30, 34, 36, and 38.

In the cerebellum the differentiation of the lips is very evident, the primary consisting of a large portion of the cerebellar plate (dorsal lamina) so that when the folding is completed the attachment of the secondary lip is carried to the vicinity of the isthmus. Figs. 6, 7 and 8.

The primary rhomboidal lips fuse in the calamus region and produce a bridge of nervous matter over the emergence of the myelocœle into the fourth ventricle. This appears as a well marked projection in sagittal sections at the meson. Figs. 24, 25 and 26.

The secondary lips in the same region have a caudal bend over the closed portion of the oblongata and may or may not fuse across the median line. When they do they form the obex, Figs. 16, 17, 24 and 26. The obex appears to be inconstant not only in man but in the lower animals as well. In three adult rabbit brains it appeared once. The obex is entirely intraventricular as is evinced by the attachment of the roof epithelium to its caudal margin. Figs. 24 and 26. In frontal sections advancing cephalad of the obex the secondary lip appears as a well marked rather vascular body which can be readily recognized by the naked eye as staining deeply, especially in advanced embryos. Figs. 28 and 31, human; Fig. 33, cat. It is usually closely fused with the oblongata, but the line of division as a rule can be identified by the entrance of vessels.

In the human foetus at term, Figs. 31 and 32, it bends sharply over into the roof of the ventricle, giving rise to two nervous laminæ which in this region form the major portion of the roof. When the roof is torn away, the margin where the

lip is fused to the oblongata remains and is known as the ligula; compare Fig. 31 with Fig. 2.

In comparing the transections, Figs. 31, 32, 33 and 34, with Fig. 17, the ventricular surface of the lip appears lying between the ala cinerea and the ligula, and is termed by Retzius the area postrema; when followed cephalad it is seen to merge into the area acustica. It is separated from the ala cinerea by a slight ridge called by Retzius the funiculus separans, which appears to be at the point of bending of the lip. According to Retzius the area postrema differs considerably in individuals, which is also characteristic of the secondary lip.

Just before the region of the lateral recess is reached, frontal sections show a commencing reduplication of the lip. Figs. 3 and 7. The lip here is folded laterad, mesad, then again laterad and finally mesad to end in the tela. In other sections these folds are seen to be fused together so that the ventricular surface comes to be narrowed to some extent. At the same time it is evident that the endymal layer is carried laterad and enclosed in the substantial nervous matter of the oblongata.

The foldings of the secondary lip are not so pronounced in the lower animals but are recognizable. In Fig. 9 a frontal section of the brain of a cat embryo ten millimetres N. B. measurement, the folding of the lip may be seen at the margin of the ventricle as a slight thickening. An analysis of this with a higher power shows a condition represented in Fig. 10.

The cells thus transferred to the ectal surface of the oblongata seem to give rise to a group of cells which appear on the sides of the oblongata in many embryos as far cephalad as the trigeminus and which may be connected with the ganglia of some of the nerves. An apparent connection was observed in relation to the auditory and it seemed from their position that they might have a possible connection with the so-called accessory nucleus of that nerve. I have been unable, however, to obtain sufficient evidence to make a positive assertion in regard to them.

At the region of the lateral recess the secondary lip un-

folds and forms an undulating lamella of considerable thickness which forms the entire ventral and mesal wall of the lateral recess. Figs. 4, 8, 29, 33, 35 and 36.

At the cephalic portion of the recess the primary and secondary lips are indistinguishable and are closely fused with the ectal surface of the restis and apparently enter into the formation of the lateral root and ganglion of the auditory. Compare Figs. 30 and 34, human, with Fig. 14, a frontal section of the brain of a pig embryo, twenty-one millimeters long, through the auditory nerve and with Figs. 15, 16 and 38, dog.

Cephalad the rhomboidal lip can be followed beyond the pons flexure, where it becomes very pronounced in the region of the cerebellum and probably gives rise in a large degree to the lateral protuberances of that organ. Figs. 7 and 8.

The connection of the rhomboidal lip with the auditory tract or acusticum seems fairly well proven. The tuberculum acusticum (dorsal nucleus) apparently corresponds to the flügelwülste, i. e., primary bend of the rhomboidal lip, and as just stated the ganglion of the lateral root is carried by the bending of the lip over the restis.

The comparison of this region in early embryos with the acusticum in some fishes, is exceedingly interesting and suggestive. The brain of *Amia* as figured by Kingsbury closely resembles the early embryonic condition of the mammalian brain in this region. The close connection in this form of the cerebellum with this portion of the oblongata is emphasized by him, which is of great interest when we consider that in mammalia, as already pointed out, the lateral portions of the cerebellum and the auditory region are probably formed from a continuous fold of the dorsal lamella, namely the rhomboidal lip.

The excursion of the primary rhomboidal lip in the region of the cerebellum, which is so marked in the human embryos, has not so far been observed in embryos of the lower Mammalia. Compare Figs. 6, 7 and 8 of the human embryos, with Figs. 9, 11, 12, 13 and 14 of the cat and pig.

It is possible that it may be in more advanced embryos of these forms. I have observed indications of it in slightly older

sheep embryos. An investigation of a complete series is needed in regard to this point.

According to His the attachment of the epithelial wall to the secondary rhomboidal lip in the cerebellar region after having been carried dorsad by the folding of the primary rhomboidal lip, becomes shifted again by the fusion of the contiguous surfaces of the two lips.

Stroud states that he is unable to obtain this impression from his observations, but believes that it becomes shifted by a process of unfolding without fusion.

I am inclined to the view of His in the matter, namely, in so far that a certain amount of fusion does take place.

In the sections of a human embryo from which Fig. 7 was drawn, the line of fusion was readily made out and is indicated in the figure. However, the fusion takes place apparently for only a short distance, and the further shifting is due to a greater proportional growth of the ectal portion of the substance of the cerebellar proton to that of the ventricular portion.

The growth of the cerebellum in the later stages is thus the opposite of that of the earlier stages, which are characterized by a greater proportional growth of the ventricular portion.

In the same manner the tent of the cerebellum is formed late in embryonic life by the growth of the ectal portions in a cephalo-caudad direction, thus producing a transverse fold. Fig. 26.

It is out of the province of this paper to enter fully into the discussion of the development of the cerebellum, and besides it would be premature with the information at hand.

But a point which has been brought out in my investigations I wish to record, namely, the existence in the human embryo, at least, of a well marked ventriculus cerebelli.

It is to be regretted that the brains from which the frontal sections were made, showing this cavity, had already been cut sagittally to the neighborhood of the meson.

This cavity is well shown in Fig. 7, of an embryo of about the seventh week, twenty-two millimeters N. B. length, and also appears in Fig. 2, of an embryo forty-two millimeters in length.

The cavity lies in the mesal portion of the cerebellum, the part to become the vermis, and while of considerable extent in the younger embryo, has in the older one become comparatively much reduced by the juxtaposition of the opposite walls. Later a fusion between the walls undoubtedly takes place, giving rise to the funnel-shaped depression as figured by Kohlmann. An attempt to homologize this cavity with that in some teleosts and birds would be interesting.

CHOROIDAL FOLD.

During the middle of the second month in the human embryo the pons flexure is instituted. It consists of a bending of the whole nervous tube, so that the extremities of the rhomboidal fossa are approximated dorsally and finally the caudal border of the cerebellum comes to lie in the vicinity of the calamus region of the medulla. Figs. 6, 11, 18, 19 and 20.

A fold in the roof is thus produced into which the mesenchyme insinuates itself and forms the plica choroidalis. Figs. 5, 6 and 11. At the same time the roof is carried laterally over the sides of the medulla forming the lateral recesses. Figs. 13 and 20. (See page 100.)

The villi are at first developed chiefly in the mesal portion of the fold and later appear in the sides of the lateral recess. At first in human embryos they are somewhat scattered over its lateral wall, but are more discreet in embryos of other animals. Compare Figs. 8 and 13. They soon coalesce to form a somewhat crescentic continuous body with its concavity cephalad, reaching from the extremity of one recess to that of the other. Later, two processes are developed, reaching caudad on either side of the median line along the roof of the body of the ventricle. Fig. 28. At the same time the choroid plexus, on account of the non-development of the mesal portion, appears to become divided between the caudal extensions. The picture now presented is that of a choroidal plexus starting in the extremity of each lateral recess, passing to the meson and then extending caudad to the extremity of the ventricle. Fig. 16.

The caudal portions form the paired choroidal plexuses of

the body of the fourth ventricle, the other those of the lateral recesses. In their course they follow that of the arteriæ post-cerebellaris.

In the lower animals the plexus in the lateral recess reaches the greatest development; in man the development in both regions is about the same.

In man, however, the plexus in the body of the ventricle has a greater proportional length and may reach caudad on the vermis as far as the pyramis.

I was at first led to believe that this development of the plexus took place beyond the limits of the ventricular epithelium but am now convinced that it does not.

In the early embryos the lateral extensions of the choroidal plexus are situated a little ventrad to the middle of the caudal and lateral wall of the lateral recess. Figs. 4, 8 and 13. Later because of the greater growth of the portion of the roof situated caudad to the plexus, and possibly partly on account of partial fusion of the roof cephalad of the plexus to the cerebellum, this portion of the roof (*velum medulare posterius*) becomes much abbreviated in comparison with the remainder. This relation holds true throughout life and the plexus is involuted along a line which closely borders the peduncle of the flocculus. Figs. 15, 16 and 29.

That the plexus forms a true part of the roof is evinced by the continuity of the epithelium over it.

Having considered the development of the margins of attachment of the roof and choroid plexus, it becomes necessary to follow the changes which take place in the roof as a whole.

THE ROOF AS A WHOLE.

In early embryos the opening between the body of the ventricle and the lateral recess is relatively wide, Fig. 18, but soon the constriction becomes more marked, so that the description of the ventricular cavity becomes naturally divided into that of the lateral recess and the body of the ventricle.

The constitution of the roof of the body of the ventricle differs considerably in man from the condition found in the lower

mammals. In man, with the exception of the choroid plexus, it consists largely of two distinct medullary laminæ which spring from the ligula on either side. Figs. 31 and 32. These nervous plates extend caudad beyond their direct attachment to the lip over the apex of the ventricle and they are here attached laterally by means of the pia, lined only by a thin epithelial layer. Fig. 31. In five brains of children at term examined especially with this in view essentially the same condition appeared in all. The epithelium continues on from the caudal margin of these plates over the pia of the vicinity for a short distance and then gradually fades away.

This formation of the roof seems to be peculiar to man. In no other animal did the roof appear otherwise than as thin membranous tela consisting of a layer of epithelium lying on the pia.

The reason for this appears in the greater development of the secondary rhomboidal lip in man.

This characteristic appearance of the roof is apparent in human embryos at the beginning of the third month. Compare Figs. 2 and 31.

As will be seen, the differences in the extent of nervous matter are even more pronounced in the lateral recesses.

Although the roof is better developed in man, it seems to be more persistent in the lower animals, and we have to turn to them to find an elucidation of the condition which appears in the caudal portion of the roof in man.

In advanced embryos of dogs, cats, pigs, sheep and also the chick, a marked caudal protrusion of the ventricle appears, which consists of the ventricular epithelium surrounded by a special condensation of the mesenchymatic tissues. This protrusion is completely closed and resembles the finger of a glove. Figs. 21, 22 and 23. The floor of this pocket springs directly from the caudal margin of the secondary rhomboidal lip, which is here folded over backward, while the walls are directly continuous with those of the ventricle. Its lumen at its commencement corresponds to the width of the ventricle and is circular in section. It terminates abruptly in a rounded extremity.

The choroid plexus extends in its roof a short distance caudad of the extremity of the vermis.

In the dog at birth the vermis has not as yet covered in the ventricle, which is still visible a short distance behind it. Trans-sections through this region appear exactly similar to those of the same region in man. There is the same extension of the choroid plexus along the under surface of the vermis. If the sections are followed back serially, or if a sagittal section is examined, it will be evident that an evagination of the ventricle has been cut, giving rise to the appearance of a break in the roof. Fig. 25. This evagination differs slightly in its relations at this stage from the condition found in the earlier ones, in that the roof of the evagination has become fused to the opposed surface of the vermis.

The floor of the evagination still remains separate from the pia of the oblongata. An explanation of this can be found in the relations of the mesenchymatic tissues which form the pia and arachnoid. In all young embryos this forms a delicate but close meshed network between the brain and the parietes of the cranium. As growth proceeds rarefactions and condensations of this network appear which arrange themselves according to fixed rules, and thus the subarachnoid spaces and the membranes are formed. Fig. 21.

It is out of the province of this paper to treat further of this subject except to state that in the region under consideration the network between the vermis and the evagination of the ventricle becomes condensed, while the other portions about the evagination become rarefied into the postcisterna. The condensed portion dorsal to the evagination forms quite a strong close meshed layer, which has been recognized and described by Hess, who attributed to it the drawing up of the choroid plexus on the vermis. In the horse he states that it is especially well developed, and below is attached to a process of pia shaped like the finger of a glove, which closes in the ventricle. He also implies that it draws out this pocket-shaped process. His impressions are seen to be erroneous from both points of view, inasmuch as the pocket is preformed, and secondly, does not

consist of pia except in its outer covering. He also describes the same glove-finger process in the sheep and in a cat embryo 100 mm. in length.

In the embryos of the animals so far mentioned, the cerebellum has not reached sufficient growth or development to cover in the ventricle and hide it from view. In the dog at birth the vermis only reaches the apex of the ventricle and the evagination of the ventricle is well marked and evident. In the adult dog the vermis reaches over both ventricle and evagination and both are hidden by it. On section, however, the evagination can still be made out, but it is flattened so that its roof and floor are in contact in places. The pia covering the ventral surface of the vermis fuses also in places with that covering the oblongata. No openings were found in the evagination.

The choroid plexus reaches to the end of the evagination but is generally weakly developed. The conditions as found in the dog may be taken as a general type for the majority of the mammalia.

Other adult types sectioned and studied microscopically are as follows :

Marsupialia : *Didelphys virginiana*. The ventricle has a marked protrusion reaching beyond the vermis, and lying in the subarachnoid space, but entirely closed, Fig. 24. The plexus in the body of the ventricle is weakly developed, while the plexus reaches an enormous size in the lateral recesses, studied by transections and sagittal sections in two animals.

Rodentia : *Lepus cuniculus* and *Sciurus carolinensis* both present the same condition, namely, practically no evagination of the ventricle and a continuous roof. In all, the brains of three rabbits were cut and one squirrel.

Primates : In all the primates sectioned, with the exception of the Anthropoidæ, a peculiar condition was found in regard to the caudal extension of the ventricular walls. Apparently the pouch becomes compressed between the mesal portion of the vermis and the oblongata and its mesal portion becomes obliterated by the fusion of the roof and floor, while the lateral portions persist along the vallis. Thus the protrusion in their

forms obtains the shape of a Y whose arms project caudally in the vallis, lying between vermis, hemisphere of cerebellum and the oblongata.

Hapalidæ: *Hapale*. Two brains sectioned. In both the caudal pouch was closed and had lateral extensions, in one extending caudad as far as the caudal extremity of vermis, in the other not so far.

Cercopithecidæ: *Macacus cynomolgus*. Pouch was present with lateral extensions, but closed. In the remaining old-world monkeys sectioned, namely, *Macacus rhesus* (two specimens), *Macacus memestrinus* and *Cynocephalus anubis*, the conditions were the same with the exception that the extremities of the lateral extensions were open. Thus there was a double metapore formation. These openings, however, were very small. Through them the choroid plexus reached into the subarachnoid cavity.

No other adult forms were sectioned microscopically. Several adult brains, however, were examined by gross methods.

As far as could be determined by this method the conditions found in the sheep, ox and cat, resembled those in the dog.

Two brains of the chimpanzee (*T. niger*) were examined. In one there was a metapore formation exactly similar to that found in man, with a caudal extension of the choroid plexus on the vermis. The other exhibited a closed pouch of only moderate extent the choroid plexus being very short, resembling the condition exceptionally found in man.

These observations corroborate those of Wilder who found a metapore in the chimpanzee, gorilla, orang and several old-world monkeys.

In the *Anthropoidæ* the vermis is relatively small as in man and it does not occlude as a rule the caudal extremity of the ventricle.

In the *Cercopithecidæ*, as before stated, the vermis does project caudad to the extremity of the ventricle and its pia fuses more or less with the pia of the oblongata. The caudal protrusion thus becomes compressed, but the tendency to metapore formation is present in the lateral portions of the sac in the ma-

jority. An investigation of embryos of these forms would be very instructive.

In the new world monkeys, so far as examined (*Hapalidæ*) there is no absorption of the sac, conforming to what was found in the lower mammalia.

In all these forms, however, the communications between the lateral recesses and the subarachnoid cavity are very large.

If we attribute a functional importance to these communications in equalizing the intra- and extra-cerebral pressure by permitting the flow of cœliolymph, we can readily see why they should not be necessary in those forms in which a large portion of the walls of the brain are membranous.

In all forms in which the cerebellum is rudimentary, there is relatively a large expanse of membranous tela in the roof of the fourth ventricle.

In some of these forms, however, there is a tendency to the formation of a sac-like caudal protrusion of the ventricle.

If the fresh elasmobranch brain be tilted so that the cœliolymph gravitates to the caudal extremity of the ventricle, a bulging in the roof at this point is produced that is quite suggestive, although no distinct protrusion is found on sectioning. In the *Holostei*, Gage has figured a distinct caudal protrusion with recurvation of the lips of the ventricle in *Amia*.

In the *Dipnoi*, Burckhardt has found a similar protrusion in *Protopterus*.

In *Batrachia* through the kindness of Dr. O. S. Strong I have been able to make an examination of the following urodele forms, *Amblystoma*, *Spelerpes*, *Desmognathus*. In them I have found no evidence of a protrusion or metapore. Gage, however, has found an opening in the caudal portion of the roof in the adult *Diemyctelus viridescens* with the eversion of the lips of the ventricle.

In the *Anura* I have sectioned tadpoles of *Rana catesbiana* and *Rana palustris*, also adults of the same species and *Rana silvatica*, and found no ventricular protrusion. In the *Reptilia* on account of the difficulties experienced in fixation and decalcification, I have so far been unable to obtain satisfactory sec-

tions of this region. I should expect in these forms to probably find a caudal protrusion of the ventricle.

In Aves I have found in embryo chicks of the tenth day and later a very marked caudal protrusion which is received in a special compartment of the skull.

In comparing the conditions in the roof of the body of the ventricle in man, with those found in the lower animals, the similarity is seen to be very striking, except for the difference already mentioned in the development and extension of the secondary rhomboidal lip.

The relation of the vermis is practically the same as is found in advanced embryos of other animals, namely, it does not extend over and cover in the caudal extremity of the ventricle. We have then the conditions which in other animals have been shown to be accompanied with a caudal extension of the roof forming a closed pouch. In the foetus at the beginning of the fifth month frontal sections of this region show the following appearances: if the sections are followed back from where they pass through the cavity of the ventricle in the first sections will be seen the floor of the ventricle, or either side the secondary lip folded laterally and extending from its margin a wall of epithelium with its pial substratum, which passes dorsad toward the cerebellum and meets with its fellow in the roof where the choroid plexus is seen. Thus we have a condition of complete cœlian circumscription. Fig. 28. Passing caudad to the apex of the ventricle we find that a complete endymal tube is now cut in whose roof the choroid plexus is still seen, and whose floor is separated from the medulla by a reflexion of the pia. Fig. 27. We have here the same picture as seen in sections of the same region in advanced embryos of the dog, pig, cat, and sheep. Figs. 22 and 23.

The walls of the tube, however, are much thinner and its caliber greater. In following the sections further caudad, the walls soon become lost, but the roof still continues fused to the extension of the pia under the cerebellum. Fig. 26.

Hess describes the brain of a child at term in which he states that the ventricle was closed by a pouch-like fold of the

pia, and remarks on its resemblance to the condition found in the horse.

Judging from his description and figure, it is evidently an instance of the condition found in the lower animals. He also describes a thinning and perforation of the sides of the pouch which throws light on the formation of the aperture.

The hypothesis that there is an evagination of the roof explains the excursion of the choroid plexus on the surface of the worm. The roof of the pouch is here supported by its adhesion to the pia of the cerebellum and consequently persists.

The variations in length of the choroid plexus may depend upon the extent of the evagination of the ventricle or upon the development of the plexus itself.

The supposition that the metapore might be the orifice of an evagination has been advanced by Prof. C. S. Minot in a communication to Prof. B. G. Wilder.¹

In comparing the above described conditions as found in the embryo with those found in the adult or child at term (for there is no material difference between them) we find that the difference exists merely in a more extensive obliteration of the lateral walls and floor of the evagination, so that its characters as a tube are lost. The numerous vessels in this vicinity encroach upon the lumen of the tube, it becomes absorbed between them, and thus arises the ragged appearance of this region.

A suspicion that there is no break in the ventricular epithelium and that the evagination becomes applied to the surface of the arachnoid is refuted not only by the facts revealed by injection but by the mesh-work of arachnoidal fibers that passes between tonsillæ, arachnoid, vermis and oblongata.

In support of the injection method, I would state that the epithelium has been found to persist only when supported by a layer of tissue sufficiently strong to withstand considerable force.

The comparatively few instances of complete closure of the ventricle may be due primarily to a short or incomplete evagination, or to secondary adhesions between the arachnoidal or

¹ B. G. Wilder: The Metapore in Man and Orang. New York Med. News, Oct. 14, 1893.

pial surfaces, the epithelium being absorbed. The evidence in favor of an incomplete evagination as a factor in absence of the metapore is, that in these cases the choroid plexus does not extend back on the vermis.

In any case we must look upon an extension of the choroid plexus into the subarachnoid cavity as evidence as to the presence of the metapore.

The metapore is essentially not an aperture in a roof but rather the disappearance of the end of a structure, so that it can be compared to the opening of a shed. Hence many of the current descriptions are incorrect.

Its boundaries are not definable in all cases since its position depends upon the amount of absorption of the epithelial tube. Its apparent boundaries are those given by Key and Retzius, namely the choroid plexus above, the membranous epithelial walls on either side, and below the posterior margin of the obex if present, otherwise the ligula. The propinquity of vessels and arachnoidal strands may give it the ragged appearance described by some.

Its resemblance to a tube has been recognized by Retzius and emphasized by Hoffman and Rauber and by C. A. Morton.

Of great interest and value as bearing upon the nature of the metapore are the appearances of the ventricular epithelium, especially in the roof and its extensions.

These changes are best followed in embryos, for in them they have not proceeded so far as to entirely obscure its characters.

The epithelium lining the floor of the ventricle is columnar and ciliated, on the secondary lip it becomes lower as it approaches the margin and loses its ciliæ. Where the roof is simply epithelial it is of a low cuboidal character.

In older embryos these changes become more accentuated. Where the roof is membranous the epithelium becomes flattened and the cells much broader, so that they approach closely the appearance of the endothelial cells of the arachnoid. In the evagination of the roof in the lower animals this appearance is marked but the epithelium can be recognized by a slightly closer

arrangement of the cells and by its taking certain stains more readily.

In the extension of the ventricle in the child at term and the adult, which forms the walls of the metapore, the epithelium gradually loses its character and can not be distinguished from the arachnoidal endothelium. There is no abrupt termination.

As to the time of the appearance of the metapore it is difficult to give exact figures. It was found by C. Hess in embryos of 7, 12, 5, 16 and 17 cm., by Retzius in an embryo of 4 mos. and by Gratiolet in one of 14 weeks. There is an element of doubt in regard to these observations, especially in the younger embryos, since the nature of the opening was not recognized. I have found it in two embryos at the end of the fourth month, the others so far studied being at too early stages. In embryos of 22 and 42 mm. the epithelium of this region appears to be very weakly developed and its continuity can only be determined with difficulty.

LATERAL RECESSES.

The lateral recesses are formed by the lateral portions of the roof of the rhomboidal fossæ, when the pons flexure is completed.

The fold in the roof formed by the flexure does not extend across the roof at the region of its greatest breadth, i.e. opposite the bend in the nervous parietes, but at a point caudad to it which later corresponds to the caudal part of the entrance to the lateral recess. Figs. 18 and 19. That is to say, the fold in the roof is essentially not similar to a fold caused by the bending of a flattened tube. Rather, the entire cephalic portion of the roof is carried caudad over the oblongata.

Thus it happens that there is no infolding of the roofs of the lateral recesses since they are carried back with the cerebellar laminæ. A reference to the figures will make the point clear. The choroidal fold does not exist as such in the lateral portions of the ventricle, the involution of the choroidal plexuses in the lateral recesses being a secondary formation and not in a preformed fold. Figs. 4, 8, 9, 13 and 14.

The primary fold which has been called the choroidal fold becomes continuous with the fold between the secondary lip and the oblongata, thus the entire lateral recess is cephalad to it. Fig. 19. If we ascribe a limiting value to this primary fold, we will have to place the lateral recesses entirely in the epencephalic segment. If sagittal sections through the region of the lateral recess are examined in embryos of man, sheep, pig, dog or cat, the cerebellar laminæ will be seen to entirely form its roof. Fig. 20. Its caudal wall, caudal portion of floor and extremity in these stages are the only membranous portions. The major portion of its floor is formed by the oblongata and its lip (rhomboidal lip). Figs. 26, 33, 34, 35 and 36.

As will be seen directly, the enlargement of the membranous portions constitutes the major portion of the lateral recess in adult stages.

As growth proceeds there seems to be a distension of the recesses which is more pronounced in the lateral portions. The walls bulge as if from some internal hydrostatic pressure. Their extremities now approach the cranial walls and come to lie in close relation with the recessus labyrinthi. Figs. 4 and 8. In man, as growth proceeds, they apparently recede from the cranial wall (Figs. 29 and 30) and fold over the sides of the oblongata, where they are finally limited by the roots of the nerves.

In the pig, dog, cat and sheep their extremities seem to fuse with the dura. Fig. 38.

Coincident with their lateral extension they grow caudally. In the lower animals the caudal bulging is not so marked as in man, where their caudal limits extend as far as a point opposite the apex of the ventricle. Fig. 28.

The entrances to the recesses share but little in the general growth, and here the original embryonic condition is nearly preserved, namely, the formation of the roof by the cerebellum. Figs. 33, 34 and 35.

As growth proceeds further the lateral recess loses its distended character and the roof and floor in many cases come in contact, except where separated by the choroid plexus, so that its cavity appears as a slit. Figs. 33, 34 and 35.

Owing to the greater development of the secondary rhomboidal lip in man, the parts of the recess which it forms are as a rule entirely retained, while in the lower mammals these parts consisting from the start only of epithelium, become lost.

In man the floor of the recess is formed chiefly from the secondary lip where it extends from the medulla at the region of greatest width. It here forms a plate of nervous matter peculiarly convoluted, which usually not only extends to the extremity of the recess, but folds on itself both at its caudal and lateral portions and so enters into the formation of the roof. In the instance where it is well developed, it may form a considerable portion of the roof as well as the floor. Fig. 37. In these cases a more or less complete pouch is formed at the extremity of the recess, which Retzius proposes to call the *Marsupium* or *Pera*. Figs. 35, 36 and 37.

In other cases the lip at its extremity does not turn over into the roof but ends as a free rounded margin. Fig. 33. In contrast to the condition found in the lower mammals the caudal part of the recess in man is, as a rule, well developed and the recess is here closed. Exceptionally the condition presented in Figs. 32, 33 and 34 is found, a condition which closely approximates that found in the lower mammals. The caudal and lateral extremity is here lost and the recess opens widely into the subarachnoid cavity. In this brain the metapore was almost completely filled by the choroid plexus (Fig. 31) which may explain the unusual size of the openings in the lateral recesses.

In a large number of brains of adults and children examined, I found the openings in the lateral recesses (foramina of Luschka) present and almost invariably they conformed to the description as given by Retzius, with the single exception figured here.

Sections of this region of the brain of children at term under the microscope show the margins of the foramen as in Figs. 35 and 36. The wall of the recess ends in a smooth rounded margin and the abrupt termination of the epithelium is readily made out.

The wall of the pocket may be more or less fused to the roots of the glossopharyngeus and vagus. The existence of this fusion has given rise to the contention that the foramina here are artifacts. Microscopical sections, however, effectually demonstrate their presence.

The roof the lateral recess caudal to the involution of the choroid plexus along the margin of the posterior medullary velum, consists in all mammals, when it exists, of a simple layer of epithelium unsupported by nervous matter. Figs. 15 and 32. In the lower mammalia there is usually a slight extension of the epithelium of the roof beyond the choroid plexus forming a lateral wall for the recess, Figs. 15 and 16, which is closely applied to the dura, and which closes in the cephalic portion of the recess. Cannieu evidently observed this arrangement and thus led to the conclusion that the recess is completely closed in all mammals.

While his observations are correct for the cephalic portion of the recess, I have found in embryos of cat, dog, pig, sheep and rat in their later stages, a complete disappearance of the caudal portion of the recess, and thus a free communication with the subarachnoid cavity. In man there is as a rule no extension of the roof epithelium beyond the choroid plexus in the lateral portion of the recess, thus the dorsal margin of the foramen of Luschka is formed by the choroid plexus. Figs. 29, 32 et. seq.

It is out of the province of this paper to enter into a discussion at length of reasons for and against the division of the third cerebral vesicle into two cephalic segments.

Several of the arguments of those advocating the division have been, it seems to me, successfully refuted by Spitzka and others.

If we divide this portion of the brain into epencephalon and metencephalon there necessarily follows a division of the cavity of the fourth ventricle into epicœlia and metacœlia; and furthermore, if we cannot make this division of the cavity the whole framework of this segmentation falls down.

A successful division of the cavity that would stand criti-

cism has, as far as I am able to ascertain, never been made.

The division into epencephalon and metencephalon has been made by reason of changes of the so-called epencephalic portion which have a late appearance, both ontogenetically and phylogenetically.

The difficulty in dividing the ventricle lies in finding the point where the transverse line should be drawn.

In the division generally accepted, this line falls at the widest portion of the lateral recesses and as the oblongata terminates at the pons flexure the line must be taken as the flexure.

Now the lateral recesses are generally included in the epencephalic segment, as is evinced by their name *parepicœlia* (Wilder).

As has already been shown, the roof of the lateral recesses is formed from cerebellum, both in embryonal and adult stages, yet the floor is formed by oblongata, consequently they can be included in neither segment. Likewise the portion of the ventricle lying between them is equally indivisible.

Reference to Figs. 12, 13, and 14 will help to elucidate this point.

In Fig. 12 the terms *epicœle* and *metacœle* are easily applicable; also they can be applied in Fig. 13, but cannot be in Fig. 14. The same can be seen in comparing Figs. 3 and 7 with Figs. 4 and 8.

The reconstructions also demonstrate the same thing, Figs. 18, 19 and 20.

Sagittal sections at the meson do not help to elucidate this point.

It may be said that we can divide the lateral recesses and relegate a portion to each segment. This, however, seems to be out of the question.

Finally, if one follows the development of the rhomboidal fossa the similarity displayed throughout cannot help but impress him that the division is artificial and needless. While the use of the terms epencephalon and metencephalon is convenient in the description of certain portions, yet it only leads to embarrassment in that of other portions.

Furthermore, it leads to misconception and error. In a recent text-book of anatomy, the author recognizing the necessity of an actual demarcation between these so-called segments, makes the statement that the third encephalic vesicle becomes constricted transversely into the fourth and fifth and that a little of this constriction remains in the adult. A misstatement like this certainly does not help a student to a true understanding of this region.

CONCLUSIONS.

1. That compared with the lower mammals the rhomboidal lips reach a greater development in man.

2. That consequently in man there is a greater development of nervous matter in the roof of the fourth ventricle and in the walls of the lateral recesses.

3. That the disappearance of the walls of the lateral recesses is of greater extent in the lower mammals.

4. That in mammalia and aves a caudal protrusion of the roof of the fourth ventricle is formed at some stage in their embryonic life.

5. That in mammalia there is a tendency to the absorption of the ventricular epithelium unless it is supported by nervous matter or by the pia of neighboring structures.

6. That in man the caudal protrusion becomes lost, giving rise to a metapore.

7. That in all Anthropoidæ there is generally a similar metapore formation.

8. That the Cercopithecidæ represent an intermediate stage between the Anthropoidæ and the lower mammals, in that there is a tendency to metapore formation.

9. That in the lower mammalia the caudal protrusion as a rule remains closed.

10. That the lateral recesses represent an intermediate area shared in equally by cerebellum and oblongata.

11. To call attention to the presence in the human embryo of a well-marked cavity between the protons of the vermis.

12. That this cavity becomes obliterated by the fusion of the opposing surfaces, and the tent is of later formation and

due to the greater proportional growth of the ectal portion of the cerebellar mass.

13. To call attention to the considerable part played by the rhomboidal lip in the formation of the acusticum.

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EXPLANATION OF PLATES.

PLATE IV.

Fig. 1. Frontal section through the rhomboidal fossa of the brain of an embryo rat (*Mus decumanus*, var. *alba*) three millimeters long N. B., near the region of the X nerve. x 60. The section is slightly oblique.

Figs. 2, 3 and 4. Frontal sections of a human embryo forty-two millimeters long. The head had previously been partially sectioned sagittally. x 6.

Fig. 5. Sagittal section of the same embryo near the meson. x 9.

Fig. 6. Sagittal section near the meson of a human embryo twenty two millimeters long. x 10.

Figs. 7 and 8. Frontal sections of the same embryo. *Fig. 7* caudad of the X, *Fig. 8* at the X nerve. x 11.

PLATE V.

Fig. 9. Frontal section of an embryo cat ten millimeters long N. B. through the ganglion of the X nerve. x 22.

Fig. 10. Amplification of the region marked Sec. rhomboidal lip in *Fig. 9.* x 450.

Fig. 11. Sagittal mesal section of an embryo pig twenty-one millimeters long. x 9.

Figs. 12, 13 and 14. Frontal sections of an embryo pig twenty-one millimeters long. Fig. 12 through choroidal fold. Fig. 13 cephalad of choroidal fold. Fig. 14 through auditory nerve. x 15.

PLATE VI.

Figs. 15 and 16. Reconstruction of a portion of the brain of a dog at birth. In Fig. 16 the cephalic portion of the reconstruction has been removed. Reconstructed from the series of sections from which Fig. 38 was taken. 9 diameters.

Fig. 17. Floor of the fourth ventricle of an adult man. After Retzius. x 2.

Figs. 18, 19 and 20. Reconstruction of a portion of the brain of an embryo pig twenty-one millimeters long. Reconstructed from the series of sections from which Figs. 12, 13 and 14 were taken. 17 diameters.

PLATE VII.

Figs. 21, 22 and 23. Frontal section of an embryo cat seventy millimeters long. x 9.

Fig. 24. Sagittal mesal section of fourth ventricle of an opossum (*Didelphys virginiana*). x 8.

Fig. 25. Sagittal mesal section of the fourth ventricle of a dog at birth. x 10.

Fig. 26. Sagittal section near the meson of the fourth ventricle of a human embryo of 130 days. x 5.

PLATE VIII.

Figs. 27, 28, 29 and 30. Transections of a human embryo of 125 days. Only the brain and enough of the membranes to show the relations are drawn. The sections are more advanced on the right side. x $7\frac{1}{2}$.

PLATE IX.

Figs. 31, 32, 33 and 34. Transections of the brain of a child at term. Fig. 31 at the calamus region. x 18. Figs. 32, 33 and 34. x 6.

PLATE X.

Figs. 35 and 36. Transections of the lateral recess of a child at term. Fig. 35, region of IX. Fig. 36, region of X. x 9.

Fig. 37. Transection of the lateral recess of a child at term. x 9.

Fig. 38. Transection of the brain of a dog at birth. The section is more advanced on the left side. x 8.

OBSERVATIONS ON THE WEIGHT AND LENGTH OF
THE CENTRAL NERVOUS SYSTEM AND OF THE
LEGS IN FROGS, OF DIFFERENT SIZES (*RANA*
VIRESCENS BRACHYCEPHALA—COPE).

By HENRY H. DONALDSON and DANIEL M. SCHOEMAKER.

CONTENTS AND SUMMARY.

Introduction.

- I. Weight of the brain and spinal cord.
- II. Ratio of the weight of the brain to that of the spinal cord.
- III. Post-mortem changes in weight of central nervous system.
- IV. Influence of water absorbed by the living frog on the weight of the brain and the spinal cord.
- V. Chart I, showing the weight of the brain and spinal cord.
- VI. Explanation of Chart I.
- VII. Method of observation.
- VIII. Table of records.
- IX. Explanation of entries in Table VII.
- X. Growth.
- XI. Weight of leg muscles.
- XII. Length of leg bones.
- XIII. Fubini's observations.

SUMMARY.

1. The males of *Rana virescens brachycephala* rarely attain a body weight above 50 grms. The females (without ovaries) may weigh 75 grams or more.

When the average of the largest males is compared with females yielding the same average weight, the males are found to have the *lighter* brain and spinal cord.

2. Spring frogs tend to lose weight rapidly when kept in the laboratory. This tendency diminishes as the season advances toward autumn.

3. In *Rana virescens brachycephala* the relative weight of the brain compared to that of the spinal cord decreases as the frog increases in size.

4. The weight of the leg muscles compared with the weight of the entire frog increases in small frogs up to about 5 grms. of body weight and then slightly decreases as the frog increases in size. In individuals of all sizes, the muscles of the thigh weigh from 1.78 to 1.80 times as much as those of the rest of the leg.

5. In frogs of all sizes, the sum of the lengths of the leg bones is a nearly constant fraction of the length of the entire frog. The proportional lengths of the several bones are also nearly constant.

INTRODUCTION.

The reason for repeating on *Rana virescens brachycephala* (Cope) a series of observations already made on *Rana catesbiana*,¹ is the simple one that the former species is much more readily obtained in this locality and hence more often used for study. In the first instance the Bull frog was chosen for examination because of the great range of size offered by it, but it was expressly stated in the paper referred to that the data obtained from the Bull-frog should not be assumed to hold good for other species of *Rana* until some evidence to that effect had been brought forward. We may say at once that the relations found in *Rana virescens brachycephala* are surprisingly similar to those found in *R. catesbiana*, in spite of some broad differences between the two forms—the most striking of which is the limited range of size in the smaller species.

The general purpose of this investigation was the same as heretofore, namely, to determine how the central nervous system changed in weight with the change in the weight of the body, and especially, of the hind legs, as it was thought that

¹ Observations on the Weight and Length of the Central Nervous System and of the Legs, in Bull-frogs of different Sizes. By HENRY H. DONALDSON. *Jour. Comp. Neurol.*, VIII, 4, Dec., 1898.

a knowledge of these relations would be necessary to an understanding of variations in the peripheral system which we hope to study later.

By way of introduction, several observations are to be noted. The frogs which we have used were all spring and summer frogs. They were taken from various localities between Southern Minnesota and Southern Illinois, but showed no local peculiarities. For that reason any further mention of localities can be omitted. In dissecting these frogs in the laboratory, it soon became evident that the heavier specimens were females. (The weight of the females was always taken without the ovaries.) In the laboratory series, the heaviest *male* was found to weigh about 45 grams, while the females ranged up to 76 grams. Through the courtesy of Mr. McCurdy, a dealer in frogs, it was possible to test this point still further. On August 2nd, 1899, Mr. McCurdy had on hand some 3000 dozen frogs, mainly *R. virescens brachycephala*. Out of this lot 100 specimens weighing 40 grams or more were selected as the largest to be found. Of these, 87 were found to be females and 13, males, thus showing a great preponderance of females among the large frogs. This result is significant because, as Table VII shows, 12 of the 22 entries below 40 grams of body weight, are males, thus leading us to expect an approximate equality in the representation of the sexes unless there was some correlation between the body weight and sex among the heavier frogs. The heaviest male weighed 53 grams, while the heaviest females in three cases, weighed 63 grams.

The observation shows that the males rarely pass the limit of 50 grams in body weight and that among the heavier individuals the females are much more numerous. So far as our previous observations on the Bull-frog go, they fail to suggest any correlation of this sort in that species. It appears therefore, that *R. virescens brachycephala* differs from *R. catesbiana* by the fact that in *virescens* the females attain a greater weight and size than do the males.

The larger number of observations here recorded were made on spring frogs—that is, frogs freshly caught in April and

May of this year. In dealing with the spring frogs as contrasted with those taken later in the season, we had occasion to observe a peculiarity not previously noted. Our custom was to get a dozen frogs, freshly caught, and work them over at the rate of a frog each day. The relation between weight of the body and that of the central nervous system soon indicated that during their stay in the laboratory the frogs in question were losing rapidly in their body weight, the weight of the central nervous system remaining, so far as we could determine, quite unaltered.

Acting on previous experience with Bull-frogs as to the manner in which frogs gain and lose water, the specimens to be examined were at this time always kept in tanks containing a few stones surrounded by shallow water, and previous experience with summer frogs had indicated that little or no change in body weight would occur under these circumstances during a period of one or two weeks.

Under these same conditions however, the *spring* frogs lose weight very rapidly. The following experiment will illustrate this point:

Four specimens of *R. virescens brachycephala* were weighed separately and numbered. They were kept in the dark in a tank through which water slowly flowed, and were weighed for twelve consecutive days at intervals of twenty-four hours. The records of the body weight at intervals of four days are given below.

TABLE I.

Showing loss of weight in spring frogs kept under favorable conditions in the laboratory.

No. of Frog.		I	II	III	IV
Weight when freshly caught	May 2	56.79	34.36	15.59	5.30
Weight	May 6	51.32	30.55	14.30	5.05
Weight	May 10	49.26	28.41	14.36	4.80
Final weight	May 14	47.28	27.89	13.85	4.87

On the morning of May 15th., a tragedy occurred. Frog No. I swallowed frog No. IV and thus closed this set of observations. There are a number of interesting changes brought out by an experiment of this sort, but we pass them here as irrelevant to our present purpose.

As this condensed table shows, the greatest loss in weight is during the first days of captivity. All the frogs lose weight, but the proportional loss is greater for the heavier individuals. The irregularities in weight shown by Frogs III and IV may depend on two things; first, the condition of the water-bladder, which was usually, though not *always*, emptied before the frog was weighed, and second, variations in the amount of water absorbed. This latter is probably much the more important factor, although as variations in this amount are largely determined by conditions existing within the frog itself, they are not readily controlled.

TABLE II.

Frog.	I	II	III	IV
Percentage loss in 12 days	16%	18%	11%	8%

The percentage loss of weight for the four frogs in question is given in Table II. These data were used to correct the body-weights of the spring frogs which had been kept for more than a day in the laboratory. The body-weight thus corrected, where necessary, is the one which appears in Table VII, given farther on.

That this loss of weight is peculiar to spring frogs which have not yet recovered from the effects of hibernation and breeding, can be shown in the following way:

On June 30th, five frogs were caught and put in the tank under the same conditions as the series tested during May. They were weighed each twenty-four hours, and we select the weights at three and four day intervals for the following table:

TABLE III.

No. of Frog.	I	II	III	IV	V
Weight when caught, June 30,	70.35	40.43	28.34	18.74	6.37
Weight July 3,	71.19	40.71	26.66	17.10	5.54
Weight July 7,	69.67	39.36	29.23	16.48	Died July 6

Numbers I and III died on the 9th of July, so Table III., contains entries for three dates only. As will be seen, Frogs I and II show a slight loss. This loss, however, is not nearly so as large that found in the spring frogs. No. III shows a gain and Nos. IV and V large losses. These small frogs were at

this time still in a condition to react like those taken earlier in the season.

A third series of five frogs was tested in September, all the conditions being the same as in the earlier observations. The record is again given at three and four day intervals.

TABLE IV.

No. of Frog.	I*	II	III	IV	V
Weight when caught, Sept. 7,	100.35	43.30	36.85	15.05	3.62
Weight Sept. 10,	102.61	41.91	36.81	14.68	3.52
Weight Sept. 14,	100.70	42.12	37.15	14.82	3.64
Weight Sept. 18,	99.30	44.58	42.08	14.64	Died Sept. 14

* *Rana virescens*, but not *brachycephala*.

In this series, Nos. I and IV lost 1% and 2.6% respectively, while the other three have gained in weight.

These observations serve to bring out the point under consideration, namely, that the large and progressive loss of body weight observed in May is a peculiarity of the spring frogs taken as they are, soon after emergence from the winter sleep, just after the breeding season, and before they have obtained much food.

In recording the results of this study of *R. virescens brachycephala*, we shall follow the same order of presentation as in the case of the Bull-frog, and also refer to the earlier paper for some details which it does not seem necessary to repeat here. In view of the recent date of the paper on the Bull-frog we shall here present the data for *R. virescens* only, and indicate briefly how these compare with corresponding data obtained from *R. catesbiana*.

I. THE WEIGHT OF THE BRAIN AND SPINAL CORD.

The proportional weight of the brain and spinal cord decreases as the body-weight of the frog increases. This is shown in the following table:

TABLE V.

Body-weight in grms.	Sex.	Weight value of Brain.	Weight value of Spinal Cord.
3.34	M.	1.43%	0.57%
38.16	M.	0.27%	0.13%
76.54	F.	0.20%	0.10%

The foregoing table is constructed from data extracted from Table VII. The body-weight as given in this and the other special tables will always serve for the identification of a record. The numbers representing the weight values of the brain and spinal cord correspond to those found in Bull-frogs of the same weights. They show that the proportional weights of both the brain and spinal cord suffer a steady diminution; the value for the brain falling the more rapidly. When the sexes are contrasted in virescens, the slightly heavier central nervous system in the female increases the percentages by a corresponding amount, but the difference does not need to be discussed in detail.

II. RATIO OF THE WEIGHT OF THE BRAIN TO THAT OF THE SPINAL CORD.

The fact that the proportional weight of the brain undergoes the more rapid decrease, brings with it the result that the ratio of the weight of the brain to that of the spinal cord diminishes as the weight of the frog increases.

Using the same cases employed in Table V, we have the following:

TABLE VI.

Body weight in grms.	Ratio of the weight of the brain to that of the spinal cord.
3.34	2.52
38.16	2.12
76.54	1.93

This series of ratios corresponds with what has been found for the Bull-frog, though for frogs of the same weight the corresponding ratios are always lower in *R. virescens*.

In the Bull-frog we have seen that a diminution in this ratio goes along with the maturing of the central nervous system, and we may therefore interpret the smaller numbers found in *virescens* as meaning that in our largest frog (of 76 grms.), the brain has already attained the same weight relation to the cord as is found in the largest of the Bull-frogs, which may have a body-weight of more than 400 grms.

Of course the records as they appear in Table VII, do not furnish a series of ratios which decrease with unbroken regularity, but if the cases as they stand in the table be arranged in three groups, the ratios not only decrease from the group with the smallest average body-weight to that with the largest, but, also in each group, fall below those for Bull-frogs of the same body weight; thus agreeing in both respects with the results given in Table VI.

III. POST-MORTEM CHANGES IN THE WEIGHT OF THE CENTRAL NERVOUS SYSTEM.

In the study of the Bull-frog we took occasion to point out the remarkable increase in the weight of the brain and spinal cord occurring when these were left in the body for twenty-four hours after death. It need only be stated that experiment shows a similar increase to occur in *R. virescens*. All our specimens, however, were dissected as soon as killed, so that our results are free from this source of error.

IV. INFLUENCE OF THE WATER ABSORBED BY THE LIVING FROG ON THE WEIGHT OF THE BRAIN AND SPINAL CORD.

When studying the Bull-frog some pains was taken to show how far the weight of the frog and of the central nervous system might be influenced by the amount of water present in the frog, and also the manner in which this water could be lost and regained. The practical outcome of these observations was the conclusion that to obtain uniform results in weighing frogs, they should be kept *in* water for some hours before they are killed.

Parallel experiments to those on the Bull-frog have been made on *virescens* with corresponding results, so that we now know this species to react like the Bull-frog. In accordance with these results care was taken that the frogs used for dissection had been *in* the water for some time before they were examined, and thus they were in the condition of having absorbed the maximum amount of water normal to them at that season of the year and under the laboratory conditions.

V. CHART I.

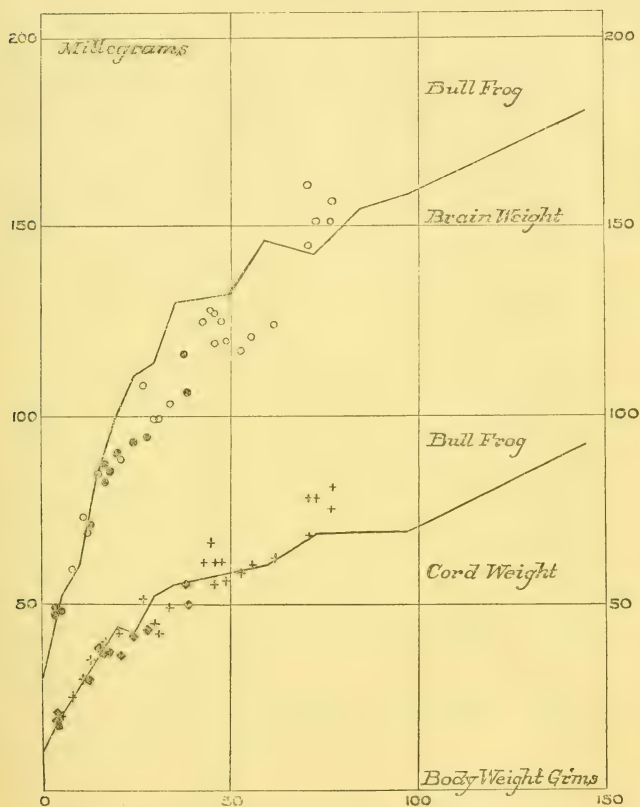


Chart I, shows by the solid lines the weight in milligrams of the Brain and Spinal Cord in Bull-frogs up to 146.9 grms. of body-weight. Compared with these are the records for *R. virescens brachycephala*. For this latter species the weight of the brain is indicated in each case by a black circle ● for the males, and a ring ○ for the females. The weight of the cord

is indicated by a black square ■ for the males and a cross + for the females.

VI. EXPLANATION OF CHART I.

The chart is based on the first part of Chart I, published for the Bull-frogs.⁽¹⁾ On this have been inserted the data for *R. virescens brachycephala*. A distinction among the records for *virescens* according to sex has been also made.

The curve for the Bull-frog is based on selected cases; on the other hand, *all* the records for *virescens* have been put down. If we compare however the two sets of results, it is in the first place evident that their general similarity is the most striking feature. If a curve based on the averages for the observations on *virescens* were drawn, it is evident that up to a body-weight of 15 grms. it would closely follow, for both the brain and spinal cord, the curve for the Bull-frog. From this point the curve for *virescens* would for a space fall below that for the Bull-frog both in case of the brain and also of the cord. At the body-weight of about 50 grms. the curve for the cord in *virescens* would pass above that for the Bull-frog, while that for the brain would rise less rapidly and to a smaller degree, thus showing the relatively high weight of the cord, to which attention has already been called. It follows also that for both divisions of the central system, the curves in *virescens* are nearer a straight line than those for the Bull-frog. When attention is directed to the records according to sex, the earlier fall in the curves for the males and hence their greater departure from a straight line, is readily seen.

VII. METHOD OF OBSERVATION.

As the methods used in this investigation were identical with those employed in the study of the Bull-frog, we will merely quote, with some slight emendations, the description as given in the earlier paper:

“Those records which involve the examination of the legs

(1) loc. cit. p. 322.

as well as the nervous system, are termed 'complete,' while those involving the nervous system only, are termed 'partial records.' In every case, however, the 'partial records' represent special observations and are not fragments of those intended to be complete."

The following account gives in detail, the manner in which the complete examination of a frog was made:

The frog was killed with chloroform or ether, and at once weighed entire. The length was taken. The legs were next separated from the body and severed at the knee and ankle joints, thus dividing each leg into three segments. Each segment was placed immediately in a closed weighing bottle.

Before weighing the segments of the leg, the brain and spinal cord were exposed, their lengths taken, and then each removed to a small weighing bottle and weighed at once.

The sex was next determined. Lastly, the weights of the stomach contents and the ovaries, when present, were ascertained and subtracted from the body-weight, as first taken.

The bottles containing the segments of the legs were then weighed separately. Next each segment was removed from the bottle and the bottle itself freed from any fluid that had collected in it. The skin, together with the bone (or bones), freed as completely as possible from the muscles and tendons, were returned to the dry bottle, which was then weighed for the second time. The difference between the first and second weighing gave the weight of the muscles of the respective segments.

The length of the leg bones was determined. This last measurement was made while the bones were fresh and moist, since they shorten on drying.

VIII. TABLE OF RECORDS.

TABLE VII.

No.	Sex	Body.		Weight of Muscles.			Length of Bones			Weight		Length	
		Weight	Lgth.	Thigh	Shank	Foot	Femur	Tibia	Foot	Brain	Cord	Brain	Cord
1	M	3.34	87	.259 .256	.078 .077	.051 .048	16.8 16.4	18.2 18.3	28. 27.8	.0475	.019	11.	10.8
2	M	3.89	97	.287 .289	.095 .090	.070 .061	16.2 16.2	18.4 18.4	28. 28.	.048	.018	10.	9.8
3	M	4.13	99	.291 .293	.104 .096	.065 .057	17.4 17.4	20.2 20.1	30. 30.	.049	.021	11.2	10.6
4	F	5.06	102	-----	-----	-----	-----	-----	-----	.048	.020	-----	-----
5	F	7.85	124	.775 .750	.267 .270	.177 .176	21. 21.	24.1 24.1	38. 37.8	.059	.025	11.6	11.9
6	F	10.90	136	-----	-----	-----	-----	-----	-----	.073	.030	-----	-----
7	F	11.41	139	-----	-----	-----	-----	-----	-----	.069	.030	-----	-----
8	M	12.32	141	-----	-----	-----	-----	-----	-----	.071	.035	-----	-----
9	F	14.85	153	1.376 1.402	.520 .519	.288 .272	26.7 27.	30.9 31.	47. 48.	.084	.038	13.1	13.6
10	M	16.26	164	1.837 1.823	.647 .630	.380 .374	28.3 28.3	32.6 32.6	50.5 51.	.087	.040	13.1	14.2
11	M	16.31	160	-----	-----	-----	-----	-----	-----	.082	.037	-----	-----
12	M	17.13	166	-----	-----	-----	-----	-----	-----	.085	.037	-----	-----
13	M	19.91	160	1.915 1.997	.731 .727	.421 .409	27.4 27.4	32.1 32.1	48.8 49.2	.090	.042	13.4	14.5
14	F	20.35	162	2.335 2.359	.838 .850	.444 .440	29.2 29.2	33.7 33.6	52.2 52.	.088	.042	14.2	14.4
15	M	23.45	168	2.680 2.666	1.019 .978	.518 .495	30.2 30.	34.5 34.5	53. 52.7	.093	.041	14.	15.
16	F	27.19	193	2.733 2.741	1.027 1.012	.621 .608	34.3 34.3	39.3 39.3	60.3 60.3	.108	.051	14.6	16.2
17	M	27.42	172	2.781 2.760	1.035 1.022	.480 .422	29.9 30.2	34.5 34.9	53. 53.	.094	.043	13.6	15.6
18	F	29.40	185	3.105 3.097	1.141 1.201	.533 .538	32.8 32.8	38.1 38.1	58.7 58.7	.099	.044	15.	16.
19	F	30.45	179	3.330 3.232	1.240 1.195	.659 .603	33. 33.	37. 37.	57.2 57.2	.099	.042	15.	15.8

TABLE OF RECORDS—CONTINUED.

No	Sex	Body		Weight of Muscles.			Length of Bones			Weight		Length	
		Weight	Lgth.	Thigh	Shank	Foot	Femur	Tibia	Foot	Brain	Cord	Brain	Cord
20	F	33.96	172	3.480 3.681	1.393 1.354	.603 .631	31.2 31.5	36.1 36.8	52.5 52.4	.103	.049	15.	15.7
21	M	36.03	198	-----	-----	-----	-----	-----	-----	.116	.055	-----	-----
22	M	38.16	200	3.637 3.536	1.563 1.456	.715 .653	35. 34.5	40.3 39.5	62. 61.	.106	.050	15.0	17.8
23	F	42.54	215	4.455 4.369	1.562 1.535	.822 .843	35.2 35.4	39.4 39.2	61.5 62.5	.125	.061	14.6	17.6
24	F	44.75	208	-----	-----	-----	-----	-----	-----	.128	.066	-----	-----
25	M	45.37	205	4.383 4.278	1.496 1.493	.869 .816	35. 34.9	39.5 39.8	60. 60.	.119	.055	15.	17.9
26	F	46.00	216	4.797 4.830	1.844 1.828	.926 .926	37. 36.8	42. 41.8	64.8 64.8	.127	.061	15.3	18.3
27	F	47.58	206	4.713 4.616	1.741 1.813	.824 .871	36.5 36.5	41.5 41.5	63. 63.	.125	.061	16.1	19.1
28	F	48.33	220	5.402 5.430	1.906 1.949	1.006 1.019	38.3 38.3	43.6 43.6	68.5 68.5	.120	.056	15.6	19.5
29	F	52.55	206	5.404 5.456	2.450 2.400	.835 .850	37. 37.	42.5 42.5	63. 63.	.117	.058	17.0	19.0
30	F	55.25	215	5.595 5.468	1.837 1.875	.917 .921	38.1 38.3	43.2 43.2	66. 66.	.121	.060	16.1	18.8
31	F	61.1	226	6.520 6.655	2.463 2.500	1.087 1.189	39.5 39.5	43.5 43.5	65. 65.	.124	.062	16.4	20.0
32	F	70.76	240	7.962 7.936	3.020 3.093	1.598 1.576	41.9 41.9	47.2 47.2	72. 72.	.161	.078	16.4	-----
33	F	70.98	239	6.741 6.731	2.520 2.427	1.551 1.436	41.4 41.4	46.7 46.8	74.6 74.5	.145	.068	16.0	18.3
34	F	72.13	246	7.621 7.530	2.814 2.780	1.405 1.366	41.9 41.9	47.5 47.5	72.8 73.8	.151	.078	16.9	21.0
35	F	76.35	248	7.059 7.137	2.633 2.572	1.349 1.301	41.5 41.5	46.2 46.	71. 72.	.151	.075	17.3	22.8
36	F	76.54	262	6.924 6.826	2.258 2.484	1.497 1.527	45. 45.	50. 50.	76.5 76.5	.157	.081	17.4	23.0

IX. EXPLANATION OF THE ENTRIES IN TABLE VII.

From this table all derived numbers such as ratios and percentages have been purposely excluded. The derived numbers appearing in the body of the paper are, however, based on the records in this table, and can be verified by means of them. As will be seen by examining the table, the various weighings were in centigrams or milligrams, as the case demanded, and lengths were taken in millimeters or tenths of a millimeter.

To facilitate the understanding of the Table, an explanation of each of the entries there found, is added.

Number.—The number is given solely for the purpose of identifying the record.

Sex.—M. Male. F. Female.

Body-weight.—The total weight of the body as taken immediately after death, was corrected, if necessary, first by subtracting the weight of the stomach contents, when this was appreciable, and second, in females, by subtracting the weight of the ovaries, when these were mature enough to show black pigment. A correction for the loss of weight in spring frogs was also made.

Length. (Lgth.)—The frog was hung by a hook through the under jaw and raised until the tip of the longer foot just touched the table. The length was then taken in millimeters from the level of the highest point of the upper jaw to the table. The two legs of a frog often differ slightly in length.

Weight of the muscles.—Thigh—shank—foot. The leg was separated from the trunk by cutting first along the faint line which marks off the skin of the thigh from that of the trunk. The proximal attachments of all the thigh muscles were then cut with a scissors and the femur disarticulated at the hip-joint.

Similarly, a separation was made at the knee-joint and at the ankle.

Each segment thus consisted of the bone or bones belonging to it, surrounded by the muscles and associated tissues, and covered by the skin.

The weight of the tissues surrounding the bones and covered by the skin—that is, the muscles, tendons, nerves and vessels—is that recorded as the weight of the muscles. The records for the left leg always stand first in the table.

Length of leg bones.—The bones were measured with a caliper square reading to 0.2 mm. In the case of the foot, the length was taken from the proximal end of the apophysis of the calcaneum to the tip of the fourth toe.

Weight of the brain.—The brain, within the limits given below, was raised on a narrow spatula, and the cranial nerves cut at their junction with it. The pia was for the most part left adherent. The choroid covering, the fossa rhomboidalis, and the hypophysis, were both removed, however, before the weight was taken.

Weight of the spinal cord.—The roots of all the spinal nerves were cut close to the cord itself, and this, still covered with the pia, was then weighed.

Length of the brain.—With spring compasses the measurement was made from the frontal end of the olfactory lobes to the caudal end of the calamus. The olfactory bulbs and tracts were thus excluded.

Length of the spinal cord.—The cord was measured in the same manner as the brain. The limits chosen were from the tip of the calamus to the point of attachment of the dorsal roots of the tenth spinal nerve.¹

The plane separating the brain from the cord thus fell a small fraction of a millimeter cephalad to the point of emergence of the first spinal nerve.

X. GROWTH.

The smallest specimens of *R. virescens brachycephala* which we obtained early in the spring, weighed about 3.4 grms.—

¹ The spinal nerves are designated according to the older enumeration I-X, and not the more recent numbering II-XI, as advocated by Gaupp in his edition of A. Ecker's und R. Wiedersheim's *Anatomie des Froches. Lehre von Nervensystem.* 1897, S. 3.

and this may be taken as indicating the minimal weight attained by this species during the first year, modified of course, by the winter sleep and spring fast.

As to the axes along which enlargement takes place in the central nervous system, the lengths of brain and cord are such in *virescens* as to give almost the same weight for the average millimeter (*loc. cit.*, Table VIII, *et seq.*) of cord or brain as appears in the Bull-frog. The similarity in this respect is very striking.

It is hardly necessary to repeat here the demonstration that the enlargement in both brain and spinal cord is much greater in the long axis than in the axes at right angles to it.

XI. WEIGHT OF THE MUSCLES OF THE LEG.

For the study of the muscles of the hind legs in *virescens*, we have 28 complete records. (See Table VII.)

For the first table given below these have been divided into four groups.

Group I includes the first 3 complete records.

“ II “ “ next 6 “ “

“ III “ “ “ 11 “ “

“ IV “ “ “ 8 “ “

In these groups the weight of the muscles of the hind leg is stated as a percentage of the weight of the entire body of the frog. The results appear as follows:

TABLE VIII.

	Proportional weight of the muscles of both hind legs.
Group I	23.5%
Group II	32.9%
Group III	32.0%
Group IV	31.3%

The muscles of the two legs never weigh exactly the same, but there is no evidence that either the right or left side is usually the heavier. In general, the numbers for the proportional weight of the muscles of the hind legs are about 2% higher than the corresponding numbers for the Bull-frog.

Group I, which is not represented in the case of the Bull-

frog, plainly contains individuals in which the legs are incompletely grown. But after *virescens* has acquired a weight of about 5 grms., the relations characteristic of maturity are seen to be attained.

In the case of *virescens*, just as in *catesbiana*, the weight value of the leg muscles undergoes a slight but steady decrease as the frog gains in body-weight. This of course, means that the body is increasing in weight at a somewhat more rapid rate than are the legs.

For the next comparison the three small frogs which constitute the Group I as given above, are so similar to those that follow them, that Groups I and II of Table VIII can be combined, with a bracket. In this rearrangement, Groups III and IV remain unchanged. The grouping now corresponds quite closely to that previously adopted for the Bull-frog.

When the weight of the muscles of the thigh is compared with that of the muscles of the remainder of the leg, the ratios are nearly constant, as is shown in Table IX.

TABLE IX.

Group.	Ratio of the weight of the muscles of the thigh	To weight of muscles of the remainder of the leg.
I. }	1.80	1
II. }		
III.	1.78	1
IV.	1.78	1

When we compare these ratios for *virescens* with those for the Bull-frog, we find first that, while the absolute value is 1.85 or more for the Bull-frog, it is only 1.80 or less for *virescens*.

In proportion to the rest of the leg the muscles of the thigh are therefore slightly less well developed in *virescens*.

The records for the two species agree nevertheless, in the fact that the proportional weight of the thigh muscles is greater in the group of lightest specimens than in the group of heaviest. The difference is however slight.

XII. LENGTH OF LEG BONES.

Still maintaining the grouping last employed, we may compare the length of all the bones of the leg taken together with

the length of the entire frog, and thus determine what percentage of this length is represented by the leg bones.

TABLE X.

Group.	Percentage of the length of the entire frog represented by the sum of the lengths of the leg bones.
I. }	68.7%
II. }	
III.	68.7%
IV.	66.8%

In this case again the *absolute* numbers for *virescens* do not agree with those for *catesbiana*—the former ranging about 2% higher. In both species, Groups I and II give the highest, and Group IV the lowest percentage, and although slight, the differences between the groups are probably significant.

To determine whether the proportions for the lengths of the leg bones are constant in the several groups, the sum of the lengths of the femur, tibia and foot can be taken as representing 100% of the length of the leg bones, and then the percentage value of the separate bones can be calculated on the basis of their respective lengths.

Treating in this manner the records comprising the several groups we obtain the proportional lengths set forth below.

TABLE XI.

Group.	Proportional lengths of		
	Femur	Tibia	Foot
I. }			
II. }	25.5	29.3	45.2
III.	25.7	29.3	45.0
IV.	27.0	30.4	42.6

The percentages for the several groups do not show any variation which can be considered significant.

These numbers indicate that in *virescens* as compared with *catesbiana*, the tibia is proportionately long, the femur and foot short, but even here the differences are small.

Summarizing the differences thus brought out between the two species, they are found to be as follows:

As compared with *catesbiana*, *virescens* has proportionally heavier hind legs, though the muscles of the thigh are lighter

in proportion to those of the rest of the leg. Corresponding with their greater weight, the proportional length of the legs in virescens is somewhat greater—considering the several bones of the leg, virescens has proportionately a slightly longer tibia, while the femur and foot are slightly shorter. All the differences in proportion are small however, and this is the more surprising since when one compares the two forms in the living state, their external appearance would not lead one to expect this close correspondence.

In general, we have to repeat the conclusion reached in the case of the Bull-frog, namely; that the weight of the leg muscles as compared with that of the entire body is the only relation that varies regularly with the size of the frog, and even in that case, the amount of variation is small.

XIII. FUBINI'S OBSERVATIONS.

In 1881 Fubini¹ published a series of observations under the title: "Gewicht des centralen Nervensystems in Vergleich zu dem Körpergewicht der Thiere, bei *Rana esculenta* und *Rana temporaria*."

To compare this study with our own, it will be necessary to summarize Fubini's work.

He examined both *R. temporaria* and *esculenta* using in all forty eight specimens of each species, there being twenty four of each sex. In all cases he determined the weight of the body and of the central nervous system (brain and spinal cord) as well as of the brain alone. The body weight in half of each species was taken without disturbing the viscera of the thorax or abdomen, while in the other half the specimens were completely eviscerated before weighing.

He concluded that in both species the relative weight of the brain and also of the entire central nervous system, was greater in the males than in the females, a relation which, he adds, is similar to that found in man.

¹ Moleschott's *Untersuchungen zur Naturlehre* etc. Bd. XII. S. 455-461. 1881.

Before showing that both these conclusions are wrong, we will indicate one or two general points suggested by his tables. These show that *R. esculenta* has a smaller brain weight than *R. temporaria*.

As an example we give below his averages of the body weight of twelve males of each species (not eviscerated) together with the corresponding averages for the weights of the brain. To these we may here add for comparison the brain weight of one specimen of *R. catesbiana* and one specimen of *R. virescens brachycephala*.

TABLE XII.

Species.	Average body weight in grams.	Average brain weight in milligrams.
<i>R. esculenta</i>	28.2	70.
<i>R. temporaria</i>	23.2	74.
<i>R. virescens</i>	27.2 (single case)	108.
<i>R. catesbiana</i>	27.3 " "	110.

The table shows the higher brain weight in *temporaria* as compared with *esculenta* and the much higher weight in both the American species.

Fubini's tables do not permit us to say anything concerning the weight of the spinal cord in the species examined by him. The reasons for this are the following: He gives, to be sure, the weight of the cord and brain taken together and then of the brain alone. He uses the term brain as we have used it and also seems to have taken the same boundaries for the cord as those employed by us. This being the case the difficulty presented by his tables may be illustrated in the following manner. For the twelve male *R. temporaria* quoted in Table XII, he gives the average body-weight as 23.2 grams; the average for the weight of the entire central nervous system as 133 milligrams and for the brain, 74 milligrams. By subtraction we get the weight of the spinal cord as 59 milligrams.

This is an impossible number and his other tables also give values in all cases entirely too large. With the frogs he examined we have every reason to expect a weight for the spinal cord which shall be not much more than half, and usually decidedly *less* than half, the weight of the brain. This expecta-

tion is based on the examination of twenty four specimens (preserved in 70% alcohol after killing by formalin) of *esculenta* and *temporaria* which we obtained from Zurich, Switzerland, for the purpose of comparison with our own species, and also from the study of the pictures of the brain and cord of the European frogs as they appear in the books, to say nothing of the evidence based on analogy with our own forms.

No explanation of this peculiarity in Fubini's tables is evident, so that the point requires further investigation.

Of course Fubini made no corrections for the probable loss of body weight in the frogs taken in the spring and this is important, as he expressly states that the observations on *R. temporaria* were made during the breeding season.

The chief source of error however, and the one which nullifies his principal conclusion, lies in his failure to appreciate the effect of the increase in the body weight of the frog on the proportional value of the central nervous system or the brain. In the four tables which he gives, the average body weight for each of the four series of females was heavier, and often much heavier, than the averages for the corresponding series of males.

This is shown by his records which we here quote in tabular form :

TABLE XIII.

Species	Condition	Average of 12 specimens Body weight in grams.			Excess of weight of females.
		No.	Males	Females	
<i>R. temporaria</i>	{ not eviscerated	1	23.2	45.6	29%
	{ eviscerated	2	20.3	26.1	
<i>R. esculenta</i>	{ not eviscerated	3	28.2	44.3	40%
	{ eviscerated	4	16.9	23.8	

In the case of the unopened frogs, Nos. 1 and 3, the ova must in large measure account for the excessive weight of the females and hence these records are useless for our present purpose. The eviscerated series Nos. 2 and 4, however, still show the average weight of the females to be the greater by 29% and 40%, respectively.

Two things follow from this: First, that in both of these species the female is in general the heavier—as we have seen to be the case in our own *R. virescens brachycephala*—and second: the influence of the heavier body of the female must be eliminated before the relative development of the nervous system according to *sex* can be stated.

We have found both for the Bull-frog and for *R. virescens* that “the relative weight of the brain and the spinal cord decreases as the body weight of the frog increases.” Table I. in the former paper and Table V. in this, may be here cited in evidence.

Let us now apply this correction to Fubini's results:

For this purpose the table of Fubini based on the eviscerated frogs can alone be used because when not eviscerated the body weights of the females were rendered worthless for statistical purposes by the presence of the ova.

Fubini's table is given below.

TABLE XIV.

Species.	Weight of Brain.	Relative Weight of Body,	
		Male.	Female.
<i>R. temporaria</i>	1.	262	291
<i>R. esculenta</i>	1.	257	287

The Table (XIV) is formed by dividing the average (eviscerated) body-weight by the weight of the brain, and hence, expressed in milligrams, it means that one milligram of brain is correlated in the first species with 262 milligrams of male body and 291 milligrams of female body.

Further, it shows that the number representing the body weight is larger for the females than for the males, and hence his conclusion that the females have proportionately the *larger* body, or, expressed in another way, the *smaller* brain.

To determine whether these ratios have any bearing on sex, apart from body-weight—which happens to be greater in the female—we select from Fubini's table (i. e. the table used to give the ratio for the male of this species in the above table XIV) of *R. temporaria*, the eviscerated males. The three smallest individuals give a body-weight of 14.9, 15.6 and 18.1

grams respectively and an average of 16.2 grams, with an average brain-weight of 69.9 milligrams. In the same manner the weights of the three specimens of intermediate size in this table give an average body-weight of 22.1 grams with an average brain-weight of 79.6 milligrams. The difference between these two averages for body-weight is 36% of the smaller number, or about midway between the two records in Table XIII. This being the case and our previous statements being correct, it follows that the proportional value of the brain in the group with heavier body-weight should be less than in the group with the lighter body-weights. The results can be best appreciated when put in the form of a table.

TABLE XV.

	Average Body-weight.	Average Brain-weight.	Ratio of Milligrams of Brain to Body-weight.
R. temporaria, (1) Males only	16.2. = (3 smallest specimens)	69.9 mgms.	1 — 231
Eviscerated, (2)	22.1 = (3 medium specimens)	79.6 "	1 — 277

Returning now to Table XIV we find the ratios of the *male* to the *female* in *R. temporaria*, as 262 to 291, the latter being thus 11% greater. The difference in the average body weights is 29% (see Table XIII). Taking the data for the *males only* of this species it appears, that within the limits of two groups of males whose average body-weights are 16.2 grams and 22.1 grams respectively, differing thus by 36%, the ratios of brain- to body-weight are 231 to 277 (see Table XV), giving a difference of almost 20% in the ratios or nearly twice the difference claimed when the two sexes were contrasted. We thus see that the males alone exhibit among themselves a greater diminution in the relative weight of the brain than do two lots of individuals grouped according to sex and differing by nearly the same amount in body-weight. The suggestion from this result as it stands, is that in the *R. temporaria* and *esculenta*, as in our own *R. virescens brachycephala*, the female has proportionately to the body-weight, a slightly *heavier* brain, *not a lighter one*, as Fubini claimed. The point can however hardly be positively decided from Fubini's data.

It will be recalled that Fubini claimed that his results obtained in the frog, i. e., the smaller proportional development of the brain in the female, corresponded with the relation of brain- to body-weight as found in man.

We have just demonstrated that Fubini was wrong in his first conclusions and that in all probability the female frog has a greater rather than a less proportion of brain when compared with the male of the *same* body-weight. As to the relation existing in man, Fubini is again in error, for Marshall¹ has shown that in the case of man, the female, despite the absolutely smaller size of her brain, has *proportionately* to her body-weight a greater mass of brain than the male.

¹ MARSHALL. Journ. of Anat. and Physiol., Vol. XXVI (N. S., Vol. VI), 1892.

A REPORT OF THE NEUROLOGICAL SEMINAR OF THE
MARINE BIOLOGICAL LABORATORY, WOOD'S HOLL,
MASS., FOR THE SEASON OF 1899.

By A. D. MORRILL.

A new and interesting feature of the fourth annual session of the seminar was the reports on experimental psychology of animals by Dr. Thorndike, who reported the results of his experiments with fishes, and by Mr. Yerkes, who reported on similar work with turtles. Both of these researches were undertaken to determine the associative power of animals and the investigation is to be extended to all the groups suitable for this method of study.

Dr. Locy reported the results obtained in his laboratory by Dr. Chas. Hill in the study of the metamerism of the head of living chick and trout embryos. The great care with which the work was done and the careful study of consecutive stages and repeated verification of the work were considered by Dr. Locy as important, as the conclusions strongly supported his own work.

Dr. Metcalf reported on that part of his work on the Tunicata bearing on the relation of the neural ganglion and the neural gland, in development. The evidence obtained tended to support the position that they arose from a common rudiment. Dr. Lefevre described the origin of the neural ganglion in budding *Perophora* and Mr. Hunter gave a demonstration of the ganglion cells in the neural gland of the adult *Molgula*, by means of methylene blue.

Dr. Lee summarized the evidence opposed to the existence of the sense of hearing in Fishes. Dr. Lyon gave some very interesting demonstrations of the compensatory movements of insects and some of the vertebrates. Mr. Prentiss described the development and adult structure of the auditory, olfactory and tactile hairs of *Palemonetes* and the innervation of the otocyst. The preparations of the otocyst demonstrated in the clearest manner the relation of the nerves to the sensory cells of the otocyst and to the brain.

The gold chloride preparations of the nerves of the earthworm by Professor Fling showed the relations of the main nerves of a segment to each other and to the nerves of the adjoining segments.

Dr. Clark reported that experimental study of the pressure sense in the human skin gave the same sensations for traction as for pressure. In hairless regions of the body these sensitive areas are often widely separated.

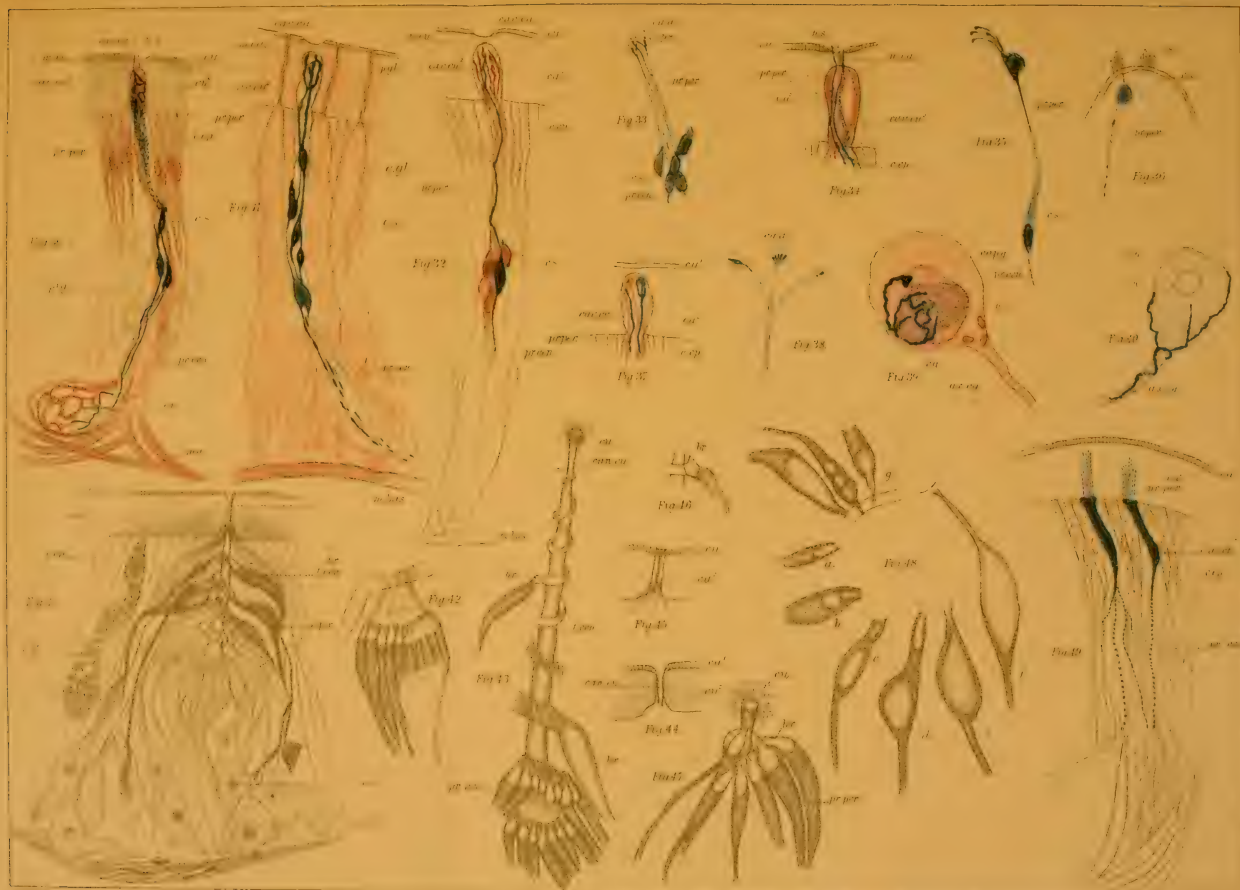
Professor Herrick in discussing the theory of nerve components pointed out the advances already made by this means of study and outlined the problems which may be solved by it in the future. The comparison of the lateral line systems of different fishes by Miss Clapp showed the common plan of distribution of the nerves and sense organs in widely different groups.

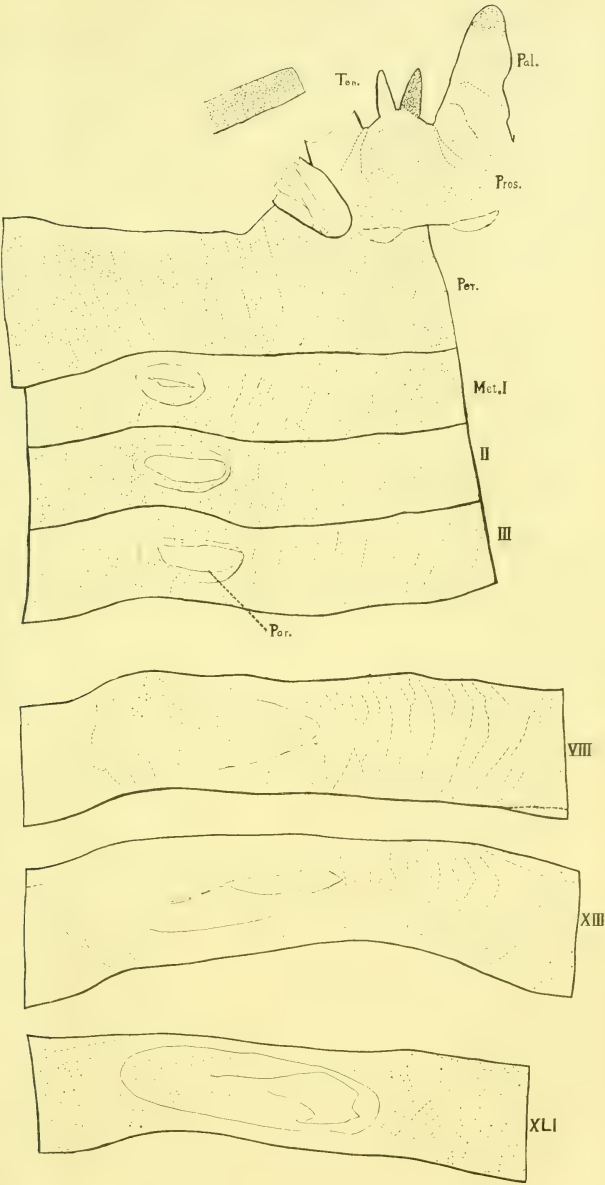
Since the papers presented were confined to original contributions, rather than reviews, only about half of those engaged in neurological work took an active part, except in the discussions, their work not being in shape to report.

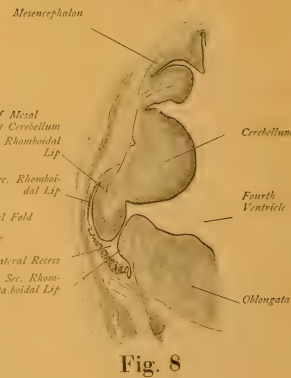
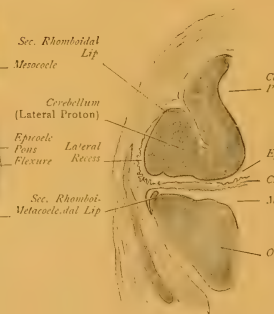
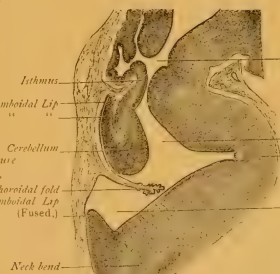
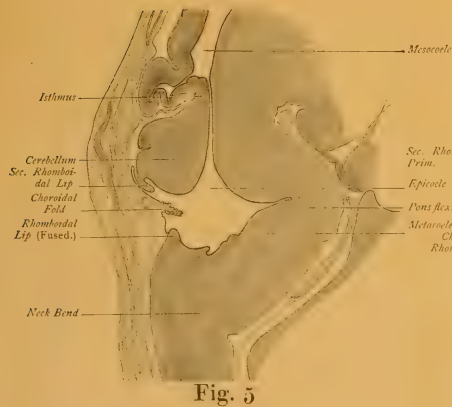
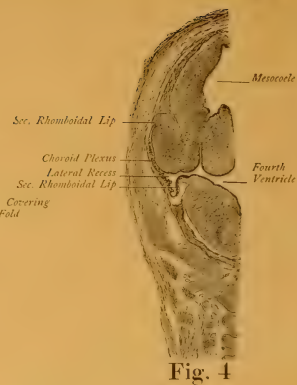
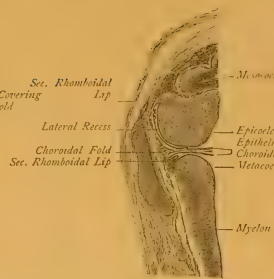
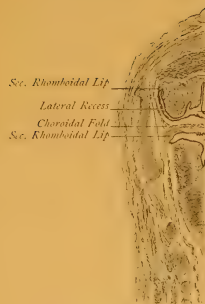
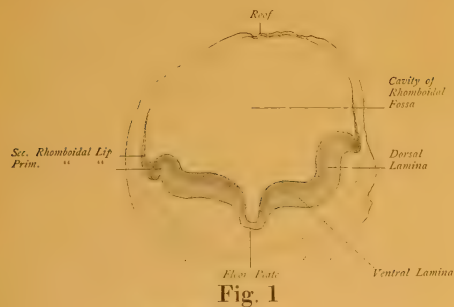
Program, Neurological Seminar for Season of 1899.

- July 11. DR. WM. A. LOCY—(Report of unpublished work of Dr. Chas. Hill). Metamerism in head of living Teleost and Bird.
- July 20. DR. M. M. METCALF—Relations of the Neural Gland and Ganglia in Tunicata.
DR. GEORGE LEFEVRE—The origin of the ganglia in budding Perophora.
- July 25. DR. F. S. LEE—Hearing in Fishes.
DR. E. P. LYON—Compensatory Movements in Insects.
- July 27. MR. C. W. PRENTISS—The Innervation of the Otocyst in Crustacea.
DR. O. S. STRONG—Some Modifications of Weigert's Method. With demonstrations.
- Aug. 1. PROFESSOR C. JUDSON HERRICK—Some Problems connected with the Theory of Nerve Components.
DR. CORNELIA M. CLAPP—A Comparison of the Lateral Line system of the Toad-fish, *Amia* and the Cod.
- Aug. 8. DR. G. P. CLARK—Pressure Sensation in the Human Skin.
MR. G. W. HUNTER, JR.—Ganglion Cells in the Neural Gland of *Molgula*.
DR. E. L. THORNDIKE—Associative Processes in Teleosts.
- Aug. 15. MR. R. M. YERKES—Associative Processes in Turtles
PROFESSOR H. R. FLING—Demonstration of some Points in the Nervous System of the Earthworm.









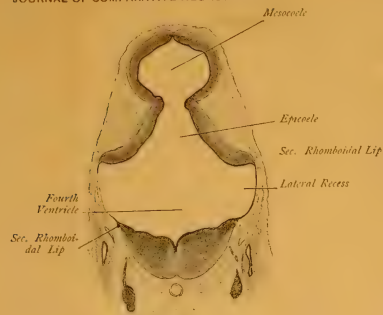


Fig. 9

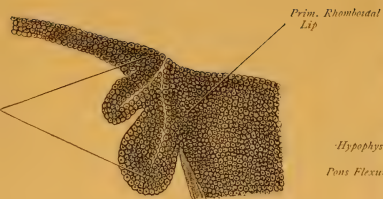


Fig. 10

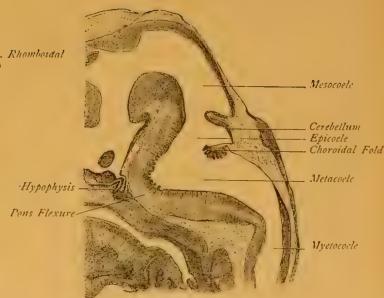


Fig. 11

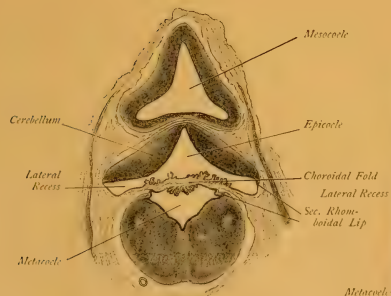


Fig. 12

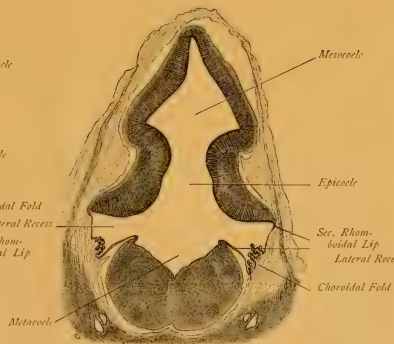


Fig. 13

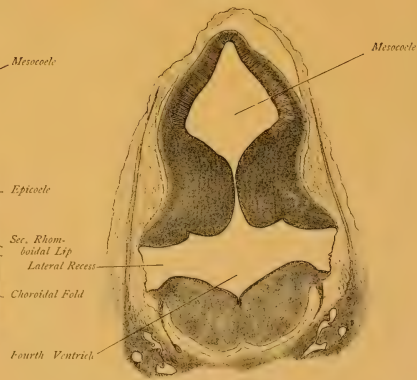


Fig. 14

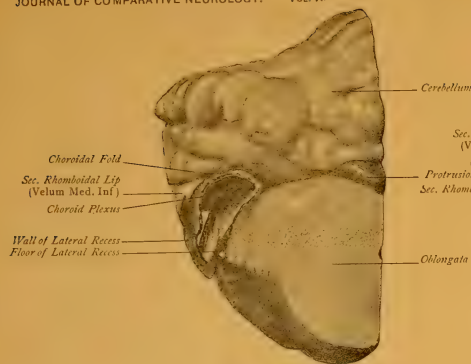


Fig. 15

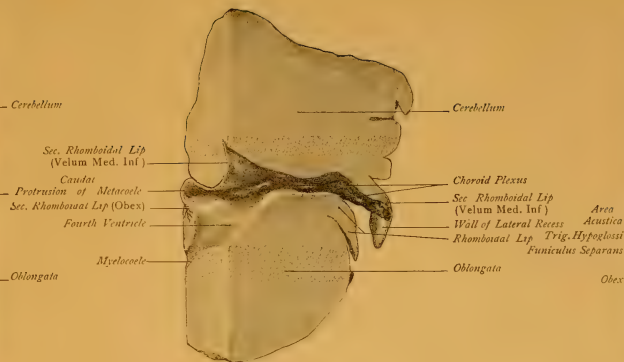


Fig. 16

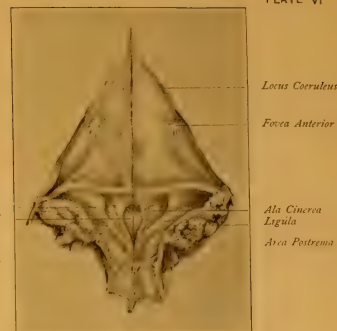


Fig. 17

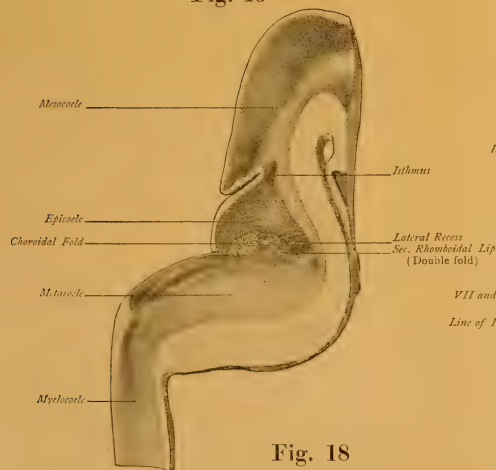


Fig. 18

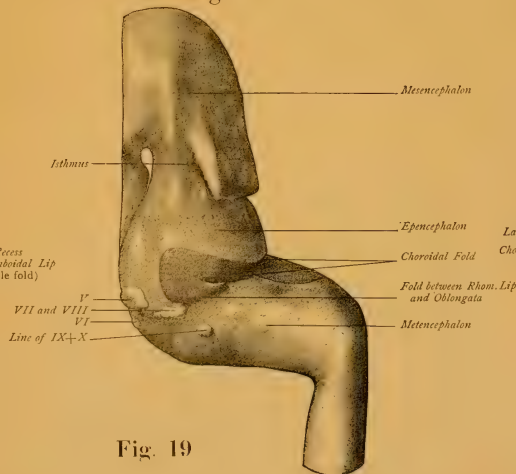


Fig. 19

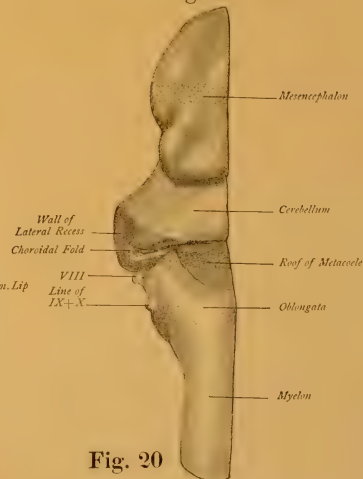


Fig. 20

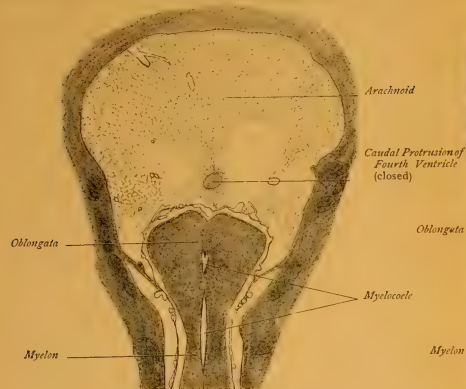


Fig. 21

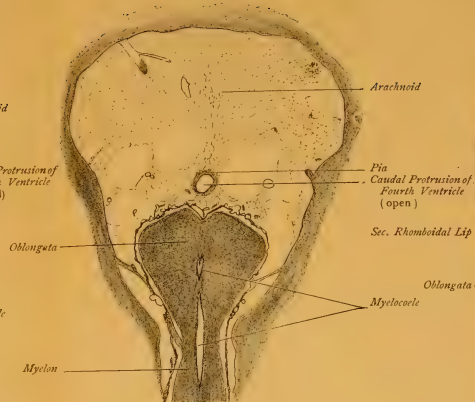


Fig. 22



Fig. 23

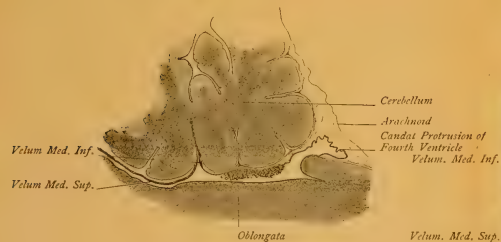


Fig. 24

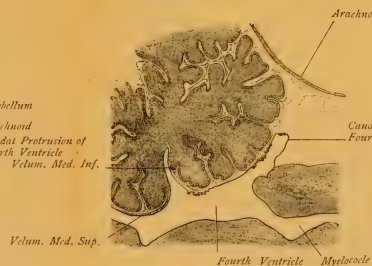


Fig. 25

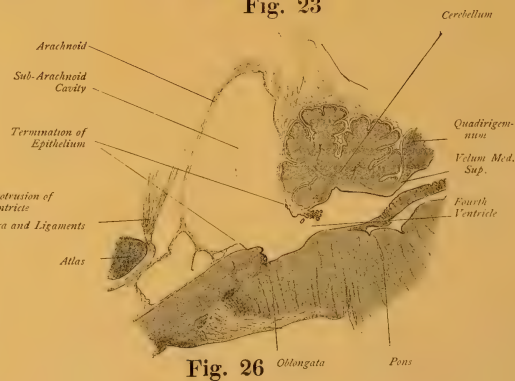


Fig. 26

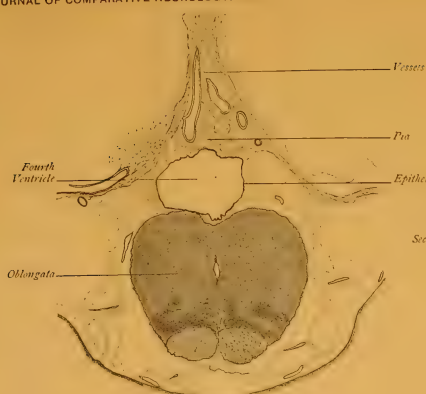


Fig. 27

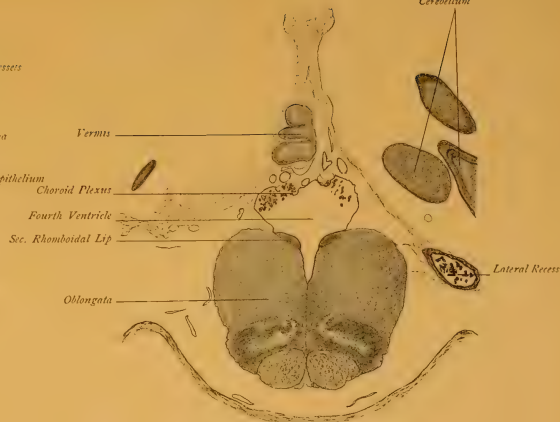


Fig. 28

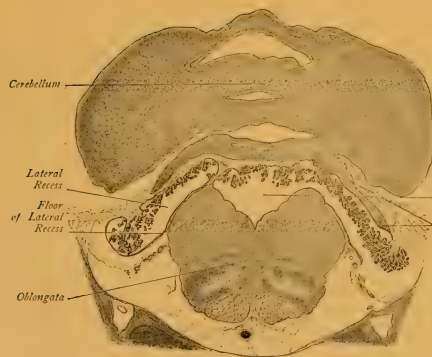


Fig. 29



Fig. 30

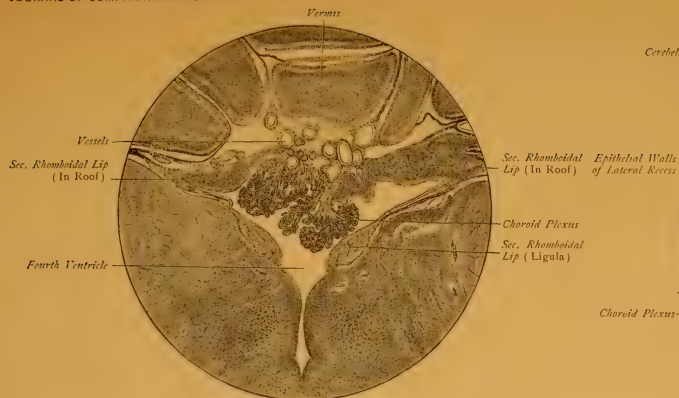


Fig. 31



Fig. 32



Fig. 33

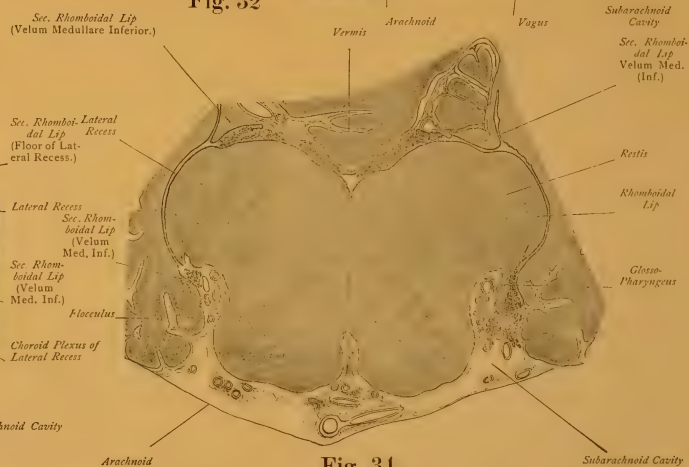


Fig. 34



Fig. 35



Fig. 36



Fig. 37

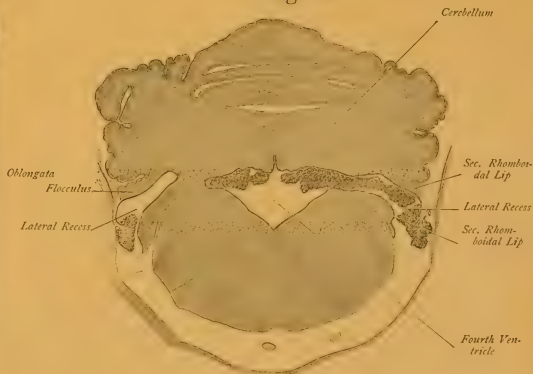


Fig. 38

THE
JOURNAL OF COMPARATIVE NEUROLOGY.

VOLUME X—NUMBER 2.

OBSERVATIONS ON SENSORY NERVE-FIBERS IN
VISCERAL NERVES, AND ON THEIR MODES
OF TERMINATING.

By G. CARL HUBER, M.D.,

*Junior Professor of Anatomy and Director of the Histological Laboratory,
University of Michigan.*

With Plate XI.

In a most suggestive paper "On the structure, distribution and function of the nerves which innervate the visceral and vascular systems," Gaskell (1) drew attention to the fact that physiological differences observed in peripheral nerves are bound up with morphological differences, so that groups of nerves of the same function can be grouped under the same morphological laws of structure and distribution. In this communication attention is drawn to the fact, that certain anterior spinal roots—namely from the 10th to the 25th—contain a relatively large number of medullated fibers varying in size from $1.8\ \mu$ to $2.7\ \mu$ and that these form the greater portion of all the nerve fibers found in the nerves commonly known as white rami; and further, that these small, medullated nerve fibers pass to the metameric sympathetic ganglia and in three main streams—upwards into the cervical sympathetic ganglia, downwards into the lumbar and sacral ganglia, and outwards into the prevertebral and terminal sympathetic ganglia. In the white rami and in the splanchnic nerves a small number of larger medullated nerve fibers were found, clearly shown in his figure (8) of a cross section of a typical white ramus as seen when stained with osmic acid. These observations corroborated in part and extended those of Bidder and Volkmann (2) who had reached the conclusion "that in the various typical nerves of

the body, the smaller nerve fibers belonged to the organic or vegetative functions of the body, and that the larger nerve fibers were concerned with its psychical activities. The former they called 'sympathetic,' the latter 'cerebro-spinal' nerve fibers. The scattered cerebro-spinal fibers found in the trunk of the sympathetic and its branches they considered to be sensory fibers."

Langley (3), in one of the first of his many important researches on the sympathetic nervous system (his observations were made on cats, rabbits and dogs), states that "when a piece of the ramus communicans, or of the trunk of the sympathetic down to the first sacral ganglion, or one of the branches running to the solar plexus or to the inferior mesenteric ganglion is teased out, after having been treated with osmic acid for a day, three sizes of medullated fibers at once catch one's attention. The fibers are about 3μ , 5μ and 8μ respectively." That the medullated nerve fibers of about 3μ or under are the visceral nerve fibers or true white rami fibers—preganglionic fibers—was clearly shown by Gaskell and Langley. Concerning the larger fibers of the sympathetic, Langley was at first inclined to adopt the view of Bidder and Volkmann, namely, that they were fibers of general sensibility. Further inquiry showed, however, that this in the main was erroneous. And while he states that: "It is well known that sensory fibers are contained in the annulus of Vieussens, in the splanchnic, and in the branches from the lumbar sympathetic to the inferior mesenteric ganglion, and that the white ramus arises from the posterior as well as from the anterior roots. Consequently, there was practically no doubt that the white rami contained sensory fibers for the sympathetic system;" he is forced to conclude, if I understand him correctly, "that many of the larger fibers, and to a varying extent in different nerves, are afferent fibers of some special sense, or subserve local visceral reflexes which escape attention under the conditions of the experiments" made by him. Edgeworth (4), in a paper which appeared about the same time as that of Langley (3) from which I have above quoted, finds in the dog's sympathetic medullated fibers 1.8μ to 3.6μ , and medu

lated fibers $7.2\ \mu$ to $9\ \mu$ in diameter; the latter he calls large sympathetic fibers. He finds no fibers of intermediary size between these two extremes, belonging to the sympathetic, but describes medullated vagus fibers $4.5\ \mu$ to $6.3\ \mu$ in diameter, which he calls large vagus fibers, and assumes that when medullated fibers of this diameter are found in the sympathetic, they come from the vagus. As the observations of Edgeworth were at variance with these recorded by Langley (3), the latter in a short communication in defence of his investigations, points out numerous errors in the work of Edgeworth (4). Of these errors it will suffice to refer only to the ones, to which attention is drawn in the following statement of Langley (5), which has reference to the large vagus fibers and their distribution: "This assumption is unfounded, since medullated fibers of $4.5\ \mu$ to $6.3\ \mu$ in diameter are present in the sympathetic in situations where there can be no question of any admixture of vagus fibers." The foregoing quotations show clearly that the investigators mentioned were able from data obtained from the measurement of nerve fibers found in cross sections or in teased preparations of white rami and sympathetic nerves fixed in osmic acid, to reach the conclusion that two distinct varieties of medullated nerve fibers were to be found in the visceral nerves—very small ones, varying in size from about $2\ \mu$ to $3\ \mu$ in diameter and larger ones from about $4.5\ \mu$ to $12\ \mu$ in diameter.

That the smaller medullated nerve fibers above mentioned are the white rami nerve fibers has been abundantly shown by the physiological experiments of Gaskell, Langley, Sherrington and others, which have been confirmed by histological observations; that the larger medullated fibers are afferent fibers, it is my purpose to emphasize.

Concerning the white rami fibers—preganglionic fibers—it is my purpose to speak very briefly, since numerous observers who have studied the sympathetic ganglia and their nerve roots have called attention to the fact that these fibers terminate in the sympathetic ganglia in intracapsular end-baskets which enclose the cell bodies of the sympathetic neurones, and this not only in the chain ganglia, but also in the prevertebral and

peripheral ganglia. "The sympathetic neurones, the cell bodies and the dendrites of which are grouped to form the sympathetic ganglia, thus become the terminal links in a neurone chain, of which the second link is formed by a neurone, the cell body of which is situated in the cerebro-spinal axis and the neuraxis of which leaves the spinal cord or medulla through the anterior or lateral root as a small medullated fiber—white ramus or pre-ganglionic fiber—which fiber ends in intracapsular pericellular baskets, enclosing the cell of the terminal—the sympathetic neurones," as I (6) have elsewhere expressed it. The neuraxes of sympathetic neurones terminate either in involuntary muscle, —non-striated and heart muscle,—in gland cells, on the dendrites of other sympathetic neurones, or in the posterior root ganglia. The neuraxes of the motor sympathetic neurones terminate after repeated division on the non-striated or heart muscle cells. Before termination the neuraxes interlace to form the intricate primary, secondary and tertiary plexuses of non-medullated, varicose nerve fibers always found in involuntary muscles when successfully stained either with gold chloride, chrome silver or methylen blue. In all involuntary muscles, whether in the heart, intestinal canal, respiratory organs, uterus, bladder, ducts of glands, blood and lymph vessels, etc., I believe the motor supply to be as above given. Neither do I possess observations which would lead me to think that other than motor sympathetic neurones take part in the formation of the terminal meshes of the above mentioned plexuses. It is evident, therefore, that the nerve cells and nerve fibers described by Schultze (7), and which he regards as a sensory end-apparatus, have not been observed by me, neither, I may say, have I seen any confirmation of his results by other observers. In heart muscle we have essentially the same general arrangement of the motor fibers. In glands, the neuraxes of sympathetic neurones form plexuses around the gland ducts and epi- and hypo-lamellar plexuses about the alveoli, the terminal branches ending on the secretory cells of the alveoli. I have digressed briefly from the immediate subject under discussion since it

seemed to me that these statements throw light on some remarks which will follow.

Nearly all observers who have investigated the sympathetic ganglia, either with the chrome-silver or methylen blue method, have called attention to the fact that in the sympathetic ganglia and nerves, as also in the white rami, neuraxes of medullated nerves larger than the white rami fibers or sympathetic fibers are to be found. These, as they have shown, pass through the sympathetic ganglia without making connection with the sympathetic neurones. That these neuraxes belong to the large "sympathetic nerves" or large medullated nerves described by Gaskell (1), Langley (3), and Edgeworth (4) there seems to me to be no doubt. That the sympathetic receives larger medullated fibers from the sensory ganglia is shown by the termination of these fibers and rests also on other data.

Langley states that the white rami receive fibers from both the anterior and posterior roots and Lenhossék has, in Golgi preparations, traced sensory fibers to the sympathetic ganglia. A statement which is found in Kölliker's (8) short account of the sympathetic system is *apropos* in this connection: "The sensory fibers of the sympathetic are finer and coarser elements which have their origin in the spinal ganglia and are distributed peripherally in the region of the sympathetic. They convey the scanty sensory impressions which emanate from the several organs. They are like certain sensory fibers in the somatic sphere, as for instance, such as end in the Pacinian corpuscles which in the mesentery have the same structure as those found in the hand and foot. All medullated fibers found far out in the periphery, i. e., those in the spleen nerves of the ruminants, in the mesentery of the intestine, in the liver, etc. I regard as sensory elements." Kölliker here indicates one mode of termination of the large medullated fibers of the sympathetic, namely the Pacinian corpuscles. These, as is well known, are numerous in the mesentery, in the peritoneum lining the posterior portion of the abdominal cavity and in and around the pancreas. That painful sensations may have their origin in the Pacinian corpuscles would seem to be shown from observations

which Warthin (9) has made. He has found the Pacinian corpuscles pathologically altered in a number of cases in which there was present diffuse and often intense abdominal pain. Of his report, attention may be drawn to two cases (VI and VII) in which there was a history of abdominal pain. Ovariectomy was resorted to as a means of relief. With the ovaries and tubes there were removed small hyalin bodies found in the mesentery. The ovaries showed only changes peculiar to the menopause and no pathological conditions were found in the tubes. The hyalin bodies proved to be pathologically changed Pacinian corpuscles. No doubt other large and small medullated nerves, especially of the hypogastric nerves, terminate in the peculiar, encapsulated sensory endings described by Timofeev (10) and found by him in the connective tissue capsule and between the muscle bundles and glands of the prostate gland of the dog and cat and in the membranous portion of the urethra of the same animals. I have seen these endings in the mucous membrane of the membranous portion of the urethra in a female cat and could readily duplicate his figures. Such special sensory nerve endings would not, however, account for all the larger medullated fibers, which we have regarded as afferent fibers, which are found in the sympathetic system. We possess, however, a number of observations which go to show that medullated nerve fibers terminate in the viscera and gland ducts in free sensory endings.

Some years ago Arnstein (11) and the writer (12) described free sensory endings in the larger ducts of the salivary glands. Ploschko (13) has described sub-epithelial and intra-epithelial sensory endings in the epiglottis, larynx and trachea. He further describes relatively large medullated fibers which pass through the sympathetic ganglia found in the trachea and end in rather compact arborizations situated in the involuntary muscle of the trachea. It was above stated that the plexuses found in involuntary muscle were formed by the division and interlacement of the neuraxes of motor, sympathetic neurones. The above apparent exception does not, it seems to me, necessitate a modification of this general statement. Since the sensory

endings described by Ploschko differ widely from the primary, secondary and tertiary plexuses found in involuntary muscle tissue, and could not be mistaken for them, I feel warranted in saying that so far as my observations go, such sensory endings in involuntary muscle tissue have not a wide distribution. I have never met with them in numerous methylen blue preparations of the intestine, bladder or gland ducts. I have dwelt somewhat fully on this observation of Ploschko, since I believe, as will appear later, that sensory nerves to the viscera do not end in the muscular coat. Berkley (14) in his account of the intrinsic pulmonary nerves of mammalia, describes nerve fibers which come from the larger nerves accompanying the bronchi—presumably medullated nerves—and pass into the folds of the bronchial mucous membrane, and end in arborizations; also nerves which end in arborizations between the epithelial cells of the smallest bronchi. These, it seems to me, must be looked upon as sensory nerve fibers of the bronchi. More complicated sensory endings found in the lung of the frog have been described by Smirnow (15); he speaks of them as “Nervenendknäuel.” They are formed by the repeated division of the neuraxes of medullated fibers, the terminal branches interlacing and anastomosing. Cuccati (16) has described similar endings in the lung of the frog. Smirnow (17) has described sensory nerve endings in the endocardium and pericardium, and Dogiel (18) has corroborated and greatly extended these observations. Ehrlich (19) in his first paper on the methylen blue method, mentions a peculiar terminal apparatus found in the bladder of the frog, to which the name “Endbäumchen” was given. The terminal arborizations found in the frog's bladder were further described by Cuccati (20) and on a former occasion the writer (6) has figured them and otherwise called attention to them. While this account was being written there came into my hands an article by Grünstein (21) working in Arnstein's laboratory, in which he gives the results of observations, made with the methylen blue method, on the innervation of the bladder in the frog, mouse, rat, cat and dog. In this article Grünstein calls attention to

relatively large medullated nerves which pass through the ganglia found in the wall of the bladder (well shown in Fig. 6, Pl. I, of his article) which end in large terminal arborizations. I hope to make further reference to his observations on the termination of the ultimate branches of such arborization somewhat later. On account of the many observations here referred to, I should not have felt a need at the present time of calling special attention to the subject under discussion, had I not found in Barker's (22) recent and most admirable volume on the nervous system, which must be looked upon as summarizing in a concise and impartial way our knowledge of the nervous system, the following statement :

“Whether or not the complex feltwork of fibers found throughout the heart have to do with the mediation of centripetal impulses or whether they are concerned wholly with the carrying of motor impulses to the heart muscle fibers has not been determined. Similar doubt exists concerning the nature of nerve endings in smooth muscle; enormous numbers of fine fibrils have been found in smooth muscle membranes, and their exact relation to the fibers has, in some cases, been carefully studied; but how many of them are motor and how many of them are sensory, remains for further investigation to determine. Certain it is that the walls of tubes which have smooth muscle coats are well supplied with sensory nerves. To make this clear I have only to mention the intestine, the bile duct, the bladder, the uterus and blood vessels.” “Whether the pain in these is the result of stimulation of sensory nerve fibers beginning in the muscle itself or in the connective tissue is not known.”

The writer has for some years made use of the methylen blue method for gaining a clearer understanding of the innervation of the various tissues and organs of examples of the different classes of vertebrates, and although the sensory visceral nerves have not been the subject of a special research, he has had frequent opportunity to study preparations which throw light on the subject under discussion and it is my purpose to give, in the remaining portion of this paper, some general conclusions reached, rather than give in detail many fragmentary ob-

servations which I have been able to make. I may state that the great majority of such observations have been made on living tissue injected with a 1 per cent. solution of methylen blue in normal salt. The tissues after the nerves were stained were fixed in a saturated aqueous solution of ammonium picrate and cleared and mounted in an ammonium-picrate-glycerine mixture. As may readily be seen, the most serviceable preparations are obtained from mucous membranes which may be studied without further sectioning, and in which, if well stained, nerve fibers may be traced for long distances, through various branchings and often to their termination.

I have previously touched on the destination of the axis cylinders of many of the larger medullated fibers found in the sympathetic nerves in speaking of their termination in the special end-organs mentioned and of their entire ending in free sensory endings. It is particularly the latter, the more common form of termination, that I desire to bring to your notice. When it is possible to trace such medullated fibers to their endings, it may be observed that before terminating they undergo repeated division before losing their medullary sheaths, such division taking place at the nodes of Ranvier, the resulting branches diverging at angles which vary greatly. This division takes place mainly in the mucosa of the hollow organs in which the nerve terminates. (In this general discussion reference is not had to the intestinal canal unless especially mentioned). The extent of this division is, I believe, greater than is generally supposed, and may, therefore, receive fuller consideration. It may best be studied in preparations occasionally obtained, in which, owing to the precariousness of the methylen blue method, only a few, perhaps only one large axis cylinder with its many branches and endings, is stained in a given region, and if, perchance, such a fiber is stained to its finest terminal branches, the extent of this division is surprising, even to one familiar with methylen blue preparations.

I have reproduced in the accompanying figure the medullated and non-medullated branches of one afferent fiber, found in the mucous membrane of the urethra of a female cat, just

distal to the neck of the bladder. This fiber was traced out with the aid of the camera lucida. In this ending twenty medullated branches may be counted, almost every one of which gives off one to several non-medullated branches before losing its medullary sheath and terminating. The area covered by the branches of this nerve I estimate to be 1.4 mm. by .8 mm. It should, however, be stated that only rarely is it possible to obtain preparations which contain endings such as here sketched. More often only a portion of such an ending seems stained or a number of them overlap to such an extent that it is impossible to trace them individually. However, in the urethra, bladder, ureters, uterus (cat and rabbit), vagina, gall bladder and bile duct, other gland ducts, and in the respiratory mucous membrane of the nose, relatively large axis cylinders, which could be traced through a varying number of divisions have been observed by me, with now and then endings as large or nearly as large as the one above mentioned; although in the bile duct and ureters I have never found such large endings. That the majority of the branches of the larger medullated nerves ending in hollow organs or gland ducts, are above the muscular coat, I think my preparations show clearly. In the one from which the accompanying figure was sketched, the muscular coat had been dissected away before mounting the preparation. Furthermore, as is well known, methylen blue stains readily non-striated muscle, so that by focusing the observer is usually able to make out the existing relations between the nerve fibers and their branches and the muscular fibers of the preparations under discussion. I do not, however, wish to be understood as saying that the medullated nerve fibers going to the hollow organs or gland ducts do not branch external to, or in the muscular coat, for this is often seen in suitable preparations, especially of the bladder wall and gland ducts; yet such branches can often be traced through the muscular coat into the mucosa, where further and more frequent division of the fibers is observed.

It may be of interest to consider, at this point, this repeated division of the large, medullated visceral nerves in con-

nection with the fact that all the earlier observers, who described large medullated nerve fibers in the white rami and the sympathetic nerves found only a few in each ramus. Gaskell (1) in his figure of a typical white ramus shows a very small number of large medullated fibers. The numbers given by Edgeworth (4), for the large medullated fibers in the white rami of a small dog, vary from 6 to 28 for the different rami examined. I infer that Langley (3) would place the number higher, although the exact numbers are not always given. Yet he states: "In the white rami there are, in most cases, more fibers larger than 4μ than are shown in the particular white ramus figured by Gaskell." It would, therefore, it seems to me, not be unreasonable to suggest that the relatively small number of medullated afferent fibers going to the viscera is in some measure compensated for by the repeated division of these fibers and by the relatively large area covered by their branches. My own observations have led me to conclude that the medullated fibers under discussion terminate, after dividing as above stated, in numerous arborizations. These, as Grünstein (21) has correctly stated, and as has been shown by me in a former paper, may be terminal arborizations—'terminales' Bäumchen—the endings of the medullated branches after losing their medullary sheaths, or lateral arborizations—'lateralen' Apparaten—the terminations of non-medullated, collateral branches, given off, at the nodes of Ranvier, from the medullated branches. The nerve fiber reproduced in the accompanying figure ends in some 45 to 50 arborizations, of which about one-half are terminal arborizations, the remainder lateral arborizations. The arborizations are formed by a subdivision of the medullated branches after losing their medullary sheaths or by a subdivision of the collateral, non-medullated branches. The ultimate branches show both in Golgi and methylen blue preparations varicosities varying in shape, size and number, and terminate in small terminal nodules or discs, which also vary in shape and size. It may not be necessary to call further attention to the fact that the afferent nerve fibers which terminate in the hollow organs and gland ducts (also in other parts of the body) end not in one arboriza-

tion but in a relatively large number of them. I have felt, however, that especially figures drawn from Golgi preparations are apt to give a wrong impression, since such figures are usually drawn from sections of tissues so stained and can, as must be obvious on a moment's reflection, give only a portion of the entire ending, at most only here and there a portion of one or several arborizations, and these usually not in connection with the larger nerve branches.

That many of the terminal branches of the arborizations here mentioned end in the epithelium it seems to me can not be questioned. Arnstein (11) and the writer (12) have shown nerve fibers in the epithelium of the salivary ducts; Ploschko (13) in the epithelium of the trachea and epiglottis; Berkley (14) in the smaller bronchi; Smirnow and Retzius (23) in the oesophagus (this Dr. DeWitt has corroborated as will be published later); Retzius (24) has described nerve fibers in the epithelium of the bladder and Grünstein (21) finds intra-epithelial pericellular nerve endings in the bladder of the cat, although in the dog, if I read him correctly, he speaks of finding only "intermusculäre Endapparate."

I have observed intra-epithelial nerve fibers in numerous preparations stained in methylen blue in which I was able to trace some of the terminal branches of arborizations, such as above mentioned, into the epithelium. Such observations, I may say, are most satisfactory if made on unfixed tissue, which after injection with methylen blue and after removal from the animal, is examined at a time when the nerve fibers have reached their maximal stain. The purplish-blue, terminal fibers may often be clearly seen between the epithelial cells, which are either only faintly stained, or if stained have a more greenish blue color. In methylen blue preparations fixed in ammonium picrate the epithelium is usually somewhat macerated, so that on mounting the preparation much of the epithelium is lost. Usually, however, some patches remain in which terminal branches of nerve fibers may be found, it must be confessed not so clearly as in unfixed specimens. Of the methylen blue preparations which I have made and examined more recently

with reference to this point I may mention the following: Bladder of the frog, cat and rabbit, in each of which terminal branches of arborizations could be traced into the epithelium; also in the urethra of cat and rabbit. In the preparation from which the figure was made, here and there intra epithelial nerves were found, although in that portion of the preparation from which the figure was drawn, very little epithelium remained; I assume, therefore, that not nearly all the terminal branches of this one fiber are shown in the figure. I believe I am warranted in drawing this conclusion by reason of the fact that in other parts of this preparation much more branched arborization may be seen, some of the terminal branches of which end in the epithelium. In a number of methylen blue preparations of the ureters of the cat and rabbit, which I have recently made for the purpose of ascertaining the mode of ending of the large medullated fibers found in their connective tissue sheath, I find plexuses of varicose fibers in the mucosa, thus inside of the muscular layer, the cells of which are usually stained. In a number of preparations only partly stained, here and there arborizations with long, slender filaments were seen in the mucosa, some of the terminal branches of which I was able to trace into the epithelial lining, this especially in preparations examined before fixing. In the uterus of the cat and rabbit, arborizations were found in the mucosa under the epithelium and in a number of these, some of the branches of such arborizations were clearly above the capillary plexus found immediately under the epithelium, and were on a level with the gland mouths, the cells of which seemed to stain more readily than the epithelial cells lining the uterus. (In these preparations, as sometimes happens, the endothelial cells of the capillaries were stained so that they could be followed nearly as well as in an injected preparation.) It seemed to me that some of the terminal branches of the arborizations were to be found in the epithelium. There is, however, room for error on this point as the thickness of the epithelium is such that by focusing it may not be possible to determine whether the terminal branches of the arborizations are in or under the epithelium. In the gall bladder and bile duct,

as Dogiel (25) has observed, there are to be found medullated nerves which do not end in the sympathetic ganglia. In the gall bladder, owing perhaps to the presence of the bile, or to the brownish stain of the epithelium, I have not been able to make out the endings of such fibers. In one methylen blue preparation of the bile duct of a cat, I was able to make out several arborizations in the mucosa—thus above the muscular coat—and from one of these some few terminal branches could be traced into the epithelium. This was in a preparation before it was fixed. It is of course well known that relatively large medullated fibers may be traced to the stomach and intestinal canal. Some of these may be traced through the ganglia of Meissner's and Auerbach's plexuses, as has been shown by Dogiel (26); this I can corroborate. I have, however, never been able to make out arborizations in the mucosa and only in a few instances and this in methylen blue preparations from the large intestine of a rabbit, have I been able to find nerve fibers which seemed to me to end in the epithelium. In these preparations, small varicose fibers, some of which were branched, others not, could be traced for short distances between the mouths of the crypts of Lieberkühn. These were seen in the same focus which brought to view the gland mouths and the epithelial lining of the large intestines; presumably, therefore, were intra-epithelial. Whether some of the nerve fibers described, and figured by Erik Müller (27) and Berkley (28) from Golgi preparations, as passing into the mucosa of the intestinal canal, are the terminations of afferent fibers I am not prepared to say; it would seem to me not unreasonable to accept this view.

By way of summary it may be stated that the larger medullated nerve fibers found in the hollow organs and gland ducts, on reaching their termination branch repeatedly before losing their medullary sheaths. This branching takes place largely in the mucosa, to lesser extent external to the muscular coat and in the muscular layer. The medullated fibers and their branches run together in various ways to form the primary plexuses. After losing their medullary sheaths, the fibers, now

non-medullated, form plexuses with smaller meshes, to which also the non-medullated collateral branches contribute. This plexus is also in the mucosa, more superficial than the primary plexus above mentioned, and therefore nearer the epithelial lining. The non-medullated terminal and collateral branches end in arborizations, many of the terminal branches of which pass into the epithelium to terminate between the epithelial cells.

Before closing I wish to mention briefly some sensory nerve endings, which I believe, should be regarded as the terminations of sensory nerves of the sympathetic; these are, however, not confined to the viscera.

Dogiel (18) has described sensory nerve endings in the adventitia of arteries and veins of the pericardium, also in the vessels of the central tendon of the diaphragm, gall bladder and the capsule of the kidney. At his suggestion Schemetkin examined the larger vessels with reference to this point and found sensory nerve endings both in the intima and adventitia, especially in the former, in the arch of the aorta and pulmonary arteries. Dogiel states that there seems to be no doubt that the sensory nerve endings found by himself and Schemetkin are found not only in the wall of the above mentioned vessels, but are characteristic of all vessels. The writer (29) has described sensory nerve endings in the adventitia of the vessels of the pia mater. I have further observed them in the adventitia of vessels in the thyroid gland in several methylen blue preparations prepared by my assistant, Dr. DeWitt. Also in other locations, though not so clearly as in the vessels of the pia mater.

It has occurred to me that the human uterus, with its large vessels and blood spaces might with profit be studied with reference to the question of the presence of sensory nerve endings in their connective tissue coats, as it seems to me not all the large medullated fibers going to this organ are accounted for by those which terminate in the mucosa and the epithelial lining.

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DESCRIPTION OF PLATE XI.

Fig. 1. Termination of a sensory nerve in the mucosa and epithelium of the urethra of a female cat just distal to the neck of the bladder.

Stained with methylen blue, fixed in ammonium picrate and cleared in ammonium picrate-glycerine.

Camera lucida drawing; 1-6 in. objective, No. 2, eye-piece, reduced to $\frac{1}{3}$.

SENSORY NERVE TERMINATIONS IN THE TENDONS OF THE EXTRINSIC EYE-MUSCLES OF THE CAT.

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With Plate XII.

In a former communication the writer (1) drew attention to a nerve-termination in the extrinsic eye-muscles of the rabbit, which differed from the motor endings found in these muscles and which for reasons there given were described as sensory nerve-endings. It is my purpose in this short paper, to call attention to a sensory nerve-ending in the tendons of the extrinsic eye-muscles of the cat which differs in many respects from the neuro-tendinous end-organs found in the tendons of other skeletal muscles of this animal.

Golgi (2) in his communications on the nerves in tendon and on the "musculo-tendinous end-organ" states that these nerve-endings have a very wide distribution, being found in practically all tendons except those of the eye-muscles. Soon after the appearance of Golgi's research on this subject, Victor Marchi re-investigated the eye-muscles with reference to this point, and in a short paper bearing on this question asserts the presence of these tendon end-organs in the eye-muscles of a number of mammals. He states having found them in cattle ('Rind'), the pig, dog, cat, rabbit and man. Marchi's description of these nerve-endings as found in eye-muscles of cattle is in its essentials as given in the following abridged and free translation.

In the transition zone between the fleshy and tendinous portion of the eye-muscles, he observed a nerve trunk coming from the muscular portion, having at times a straight course, at

other times a spiral course, which divided into two to four branches, each branch ending in a spindle-shaped structure, which from its reaction to the stains used could readily be distinguished from the surrounding tendon-bundles. These spindle-shaped structures were surrounded by a transparent sheath. Spindles branched at either the central or peripheral end, were observed. Soon after entering the spindles, the nerve-fibers divide into two, three, or even more diverging branches, which sooner or later lose their medullary sheath and as non-medullated fibers approach the periphery of the spindles where they may end abruptly or terminate between small granules found in their superficial portion. The further division and the exact termination of the nerve-fibers he was not able to make out. In each tendon four to six endings were found. As in any one tendon not all the nerve-endings may have been stained, the number above given may be too low.

I have given thus fully Marchi's account of the nerve-ending in the tendons of the eye-muscle of cattle, as in other mammals examined with reference to this point identical end-organs were found, as the following quotation which follows the above statement, will show: "Ich dehnte nach und nach meine Untersuchungen auf die Augenmuskeln anderer Thiere aus und fand bei allen die Terminalkörper in derselben Form und Grösse wieder, so dass die den verschiedenen Thierarten entnommenen Präparate gar nicht von einander zu unterscheiden waren." As in the earlier portion of his paper he mentions the cat as one of the animals which came within range of his investigation, it is permissible to assume that the nerve-endings found by him in the tendons of the eye-muscles of the cat were in shape, size and structure like the nerve-endorgan above described.

Ciaccio (4) mentions and figures the neuro-tendinous end-organs in the eye-muscles of man, but does not give special consideration to those found in the cat. My own observations were made with the methylen blue method. Through a canula inserted into one of the carotid arteries a 1 per cent. solution of methylen blue in normal salt was injected until the eye-lids

and conjunctiva assumed a distinctly blue color. Some 30 minutes after the injection the eye-muscles were exposed by removing the bony wall of the orbit, and by dissecting away the fascia and adipose tissue covering the eye-muscles. As soon as the muscles and tendons were exposed they were removed and transferred to a slide moistened in normal salt, care being taken to cut the tendons as near their ocular insertion as possible and to place them on the slide with the ocular side downwards. The muscle remained on the slide until, on examination with the microscope, the nerve-endings seemed well stained. The tissue was then fixed, either in an ammonium picrate solution and mounted in ammonium picrate glycerine, or in ammonium molybdate (Bethe). Tissues fixed by the latter method were embedded, sectioned and counter-stained in alum carmine and mounted in balsam.

In preparations prepared by the former method it is possible to mount an entire eye-muscle—fleshy mass and tendon—and yet have a preparation thin enough to study with high powers. I found such preparations most useful for ascertaining the general distribution of the nerves in the muscular and tendinous portion, their branching and their relation to the nerve-ending to be described; also the arrangement of the terminal branches of the nerves in the end-organs. Some of the details of the structure of the end-organs and the relation of the terminal nerve branches to the tissue elements were best studied in sections made as above indicated.

In preparations made after the former of the above mentioned methods, two varieties of nerve fibers (recognized by their terminations) and endings may be readily made out. Motor fibers, the endings of which are found in the middle of the fleshy mass, and rather small medullated nerve fibers, which run forward between or over the muscle fibers to the tendinous portion of the muscles, there to end in special end-organs. Similar observations have been made by Sherrington (5), as may be seen from the following statement taken from one of his papers: "I was struck with the long distance to which many of the nerve fibers in these muscles travel forward

toward the ocular tendons of the muscles. I was more impressed with this fact because direct examination proved that the region of the distribution of the motor end-plates in these muscles is almost confined to the middle portion of the fleshy mass of the muscles. Further investigation of the course and destination of the nerve-fibers at the tendon end of the muscles revealed them (both in cat and monkey) undergoing terminal sub-division and in very numerous instances passing beyond into the bundles of the tendon itself. The termination of many of the bundles of the nerves lies within the tendon; many re-curve again toward the muscular fibers and end just at the junction of the muscle fiber with the tendon bundle."

The motor endings need no further consideration as they present no structural peculiarities.

The nerve fibers terminating in the tendinous portion of the eye-muscles pass forward beyond the region of the motor endings, as small bundles consisting of two, three, four or even more small medullated fibers. The small bundles have a rather direct course, passing forward between the muscle fibers, approaching the surface of the muscle some distance before the tendon is reached. Three such small bundles are represented in the accompanying figure. After leaving the fleshy portion of the muscle, these bundles pass forward into the tendon for a short distance, usually on its outer surface, although now and then in the substance of the tendon. The termination of these fibers is in end-organs situated for the most part just beyond the fleshy portion of the muscles. One or two nerve-fibers go to each end-organ. Many nerve fibers pass forward beyond their point of termination for a short distance, to recurve again toward the muscular fibers before ending, as Sherrington (5) has correctly stated. Others approach the end-organs more directly, entering them either at their distal (which seems to me the more common) or their proximal ends. As the nerve fibers approach the end-organs, the internodal segments become shorter (this Sherrington has observed); the axis cylinders do not, however, become thicker. In this respect my observations do not corroborate Sherrington's (5) if, in the following state-

ment, he has reference also to the axis cylinders: "The nerve-fibers in so terminating frequently become thick . . . with shortened internodes." The bundles of small medullated fibers, as also the single fibers, are surrounded by a distinct fibrous sheath—a sheath of Henle.

The end-organs in question (which, as may here be stated, are simple neuro-tendinous spindles) consist of a tendon fasciculus surrounded by a thin, closely fitting fibrous sheath in which oval or oblong nuclei are found. (The sheaths surrounding the tendon fasciculi are not shown in the figure; they are not clearly seen in preparations mounted in ammonium-picrate-glycerine; they are, however, readily made out in sections of tissue fixed in ammonium molybdate.) This sheath becomes indistinct at the central and peripheral end of the end-organs and seems to blend with the fibrous tissue found between the tendon fasciculi and muscle fibers. The shape of this end-organ is more that of a cylinder than a spindle, as neither the tendon fasciculus nor the space between it and the sheath, which in all parts is narrow, are perceptibly thickened in the equatorial region. As above stated, one or two medullated fibers terminate in each end-organ. They pass through the fibrous sheath as medullated fibers with short internodes, losing the medullary sheath soon after entering. The naked axis cylinders then break up into several divergent branches, which undergo repeated further division, the resultant branches bearing the character of non-medullated fibers with numerous irregular varicosities of variable size. These terminal branches become so interlaced and interwoven that in a well stained preparation it becomes very difficult to follow them. I have attempted to reproduce these endings in the accompanying figure, to which the reader is referred in lieu of a more detailed description. This plexus is spread out over the tendon fasciculus, but under the fibrous sheath surrounding it. Some of the terminal branches penetrate the tendon fasciculus for a short distance, as may be seen in cross-sections.

The nerve termination here described differs in many respects from that found in the neuro-tendinous spindles found in

other skeletal muscles of the cat, and while there may be some similarity between the two varieties of endings, this seems not as close as the following statement of Sherrington (5) might indicate: "This terminal arborisation which the nerve-fibers finally make is, as a rule, small as compared with the end-arborisations of the ordinary Kühne-Ruffini 'spindle' or the Golgi 'tendon organ' but closely resembles in numerous instances the form of arborisation of the latter."

The end-organs here described have been found in all the recti and obliqui eye-muscles of the cat, so far never in the retractor of the bulb. In my preparations they have been relatively more numerous in the superior rectus than in the other eye muscles. This may, however, be due to the fact that the nerve-fibers and endings seemed always best stained in the superior rectus. In a number of my preparations I have been able to count some 25 to 30 end-organs in one muscle. In such preparations there is nearly a continuous band of end-organs across the entire tendon, just distal to the fleshy portion of the muscle, a band in which the end-organs are quite as numerous as in the small portion of tendon reproduced in the figure.

It is of interest to note that the nerve fibers ending in these end-organs are not branches of the ophthalmic division of the trigeminus, but that the III, IV and VI nerves, although purely muscular, must be sensori-motor. This the excellent and painstaking experiments of Sherrington (5-6) would seem to show conclusively.

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DESCRIPTION OF PLATE XII.

Fig. 1. A portion of the fleshy and tendinous portion of the superior rectus muscle of the eye of a cat, showing the course and termination of sensory nerve fibers as seen when stained with methylen blue, fixed in ammonium picrate and mounted and cleared in ammonium picrate-glycerine.

Camera lucida drawing; 1-6 in. objective, No. 2 eye-piece; reduced to one-third.

A CONTRIBUTION ON THE NERVE TERMINATIONS IN NEURO-TENDINOUS END-ORGANS.

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With Plates XIII to XVIII.

Some years ago, the writers undertook a series of researches on the innervation of muscular tissues in the belief that many of the points still in dispute concerning the termination of the nerve fibers and their relation to the elements of the tissue might receive further elucidation, if, in such investigation, the nerve fibers were stained differentially by means of a method or methods which would admit of the making of thin sections of the tissues to be studied. The method selected was the intravital methylen blue method, using ammonium picrate and ammonium molybdate as fixatives. We have thus far presented observations on the motor endings in voluntary muscle, heart muscle and involuntary muscle, sensory ending in the neuromuscular spindles, sensory ending in the extrinsic eye muscles of the rabbit, and sensory endings in the tendons of the extrinsic eye muscles of the cat.

In the present contribution it is our aim to give the results of extended observations on the ending of nerves in the neurotendinous end-organs which, both from an anatomic and physiologic standpoint, must be and are regarded as end-organs associated functionally with muscular tissues. This investigation embraces observations made on neuro-tendinous end-organs of

the frog, tortoise, bird, rat, rabbit, cat and dog. Our mode of procedure was in each case as follows:

A 1 % solution of methylen blue in normal salt was injected into the artery supplying the region in which the neuro-tendinous end-organs to be studied were situated, until the part assumed a distinctly blue color. Some thirty minutes to one hour after the injection, the muscles and tendons to be studied were quickly exposed and removed to a slide moistened with normal salt and were then placed in one or the other of the fixatives mentioned, as soon as the nerve terminations were clearly seen under the microscope. Many end-organs from each of the above mentioned vertebrates were, after staining in methylen blue, fixed in ammonium picrate and cleared in glycerine-ammonium-picrate; the ending was then carefully teased out under the dissecting microscope and mounted in the glycerine-picrate solution.

By this method, preparations are obtained, in which the general structure of the nerve-ending, its relation to the tendon fasciculi and muscle fibers and the general distribution of the nerve fiber or fibers terminating in the ending, as also the configuration of the ultimate ending of the nerves, may be readily made out. Other neuro-tendinous end-organs were, after staining, fixed in ammonium molybdate, dehydrated, embedded in paraffin and sectioned, transversely or longitudinally; the sections were then fixed to the slide or cover glass and counterstained in alum carmine. In such preparations, the relation of the ultimate ending of the nerve-fibers to the other structural elements of the end-organs is clearly brought out. Some few end-organs, after staining and fixing in ammonium molybdate and after dehydration, were cleared in xylol, teased, and mounted in balsam.

The literature bearing on nerve terminations in tendinous tissue may appropriately be divided into observations antedating and those following a communication on this subject, which we have from the pen of Golgi, to whom must be given the credit of first recognizing in tendon a special nerve end-organ.

Rollet, as early as 1876, drew attention to a nerve plexus

and a nerve network in the musculus sterno-radialis of the frog. After describing in detail the procedure used for exposing and removing the muscle and the methods employed in bringing to view the nerve fibers and endings (dilute hydrochloric acid, nitric acid, osmic acid and gold chloride), the author describes a plexus of medullated fibers and a termination which he designated as "*Nervenschollen*." These endings, he states, are in the substance of the tendon and have many points of resemblance with the end-plates of striped muscle fibers. That Rollet had before him the neuro-tendinous endings of the frog, can hardly be questioned from his description and from the figures given. The methods employed by him revealed, however, little else than the medullated portions of the nerve fibers going to this ending.

Contemporaneously with the above communication, appeared one by Sachs, who, at the instigation of Kühne, in whose laboratory the research was carried on, examined tendons of the frog, salamander, sparrow, rat and cat. In the frog, nerve fibers were found in the musculus sterno-radialis and musculus semi-tendinosus. In the salamander, nerve fibers were found in several tendons; in the sparrow, the leg and wing tendons were examined with negative results. In the mouse, nerve fibers were readily demonstrated in the long tendons of the tail, near the insertion of the muscle fibers into these tendons, and also in the diaphragm; in the cat also in the tendons of the tail and a few in the patellar tendons. In these tendons, cleared in dilute mineral acids, the nerve fibers could be traced until they lost their medullary sheaths and the figures given by Sachs show that he recognized the branching of medullated fibers in the nerve-ending in question.

With the gold chloride method, this investigator obtained a number of preparations, especially from the salamander and frog, which he interpreted as showing the ultimate ending of the nerves in tendon. Several types of endings are mentioned: one in which the medullated nerves end in an interlacing network of fine fibers, ("Die markhaltigen Endzweige der Faser

lösen sich in ein wirres Gestrüpp markloser Aestchen auf, die nach allen Richtungen sich myceliumartig verfilzen").

Another form of ending to which Sachs assigns a secondary position was found in the tendons of the frog. As the description given by him approached one which may now be given of these endings as found in the frog, we give it in his own words: "Es finden sich nämlich einzelne Fasern, namentlich in Froschsehnen, welche pinsel-förmig in eine Anzahl sehr feiner, blasser Aestchen ausstrahlen. Die letzteren sind mit wenigen spindelförmigen Kernen versehen, und verlaufen über grössere Strecken des Präparates ohne sich weiter zu verästeln. Sie endigen wahrscheinlich Spitz."

To the nerves terminating in tendon, Sachs ascribes a sensory function, believing that they subserve the muscle sense.

Gemt's investigations on nerve-endings in connective tissue did not materially further our knowledge concerning this question. His investigations on the nerve endings in tendons of mammalia gave negative results. Concerning the nerve endings in tendons of frogs and lizards, he says: "From the several medullated branches of the nerves going to tendon, there proceed varicose fibers of variable size, which branch often and now and then anastomose; these end free in the tissues without any terminal enlargement."

Golgi's observations on this subject were much more comprehensive and must be regarded as fundamental to our more accurate knowledge of the special sensory end-organs in tendon, especially with reference to those found among the higher vertebrates. His own summary of the literature preceding his publication may be here inserted, as it states comprehensively the status of the question under consideration at the time he began his work. He says: We may say, therefore, that while we possess a fairly detailed knowledge concerning the nerves ending in the tendons of lower vertebrates (frog and lizard), concerning the problem of the connection of the nerves with the tendons of higher vertebrates in general and man in particular, our knowlege has not been materially advanced since Kölliker stated that he had observed in the tendons of small

bats, numerous nerves spreading out superficially. In larger tendons of man, tendo Achillis, tendon of quadriceps extensor and central tendon of diaphragm, the nerves enter with the blood vessels. In fascias, tendinous sheaths, and synovial sheaths, he had discovered no nerves.

Golgi's observations extended over those made on the tendons of man and several other mammals (rabbit, dog, cat and mouse), birds (sparling, finch and swallow), amphibia (frog) and reptilia (lizard). For reasons above given, they will be considered somewhat fully.

In the lizard, tendon endings were found by Golgi in muscles of the anterior and posterior extremity and in several small tendons belonging to muscles of the vertebral column and tail. The endings were found near the muscular end of the tendon. The nerve fibers terminating in tendon could usually be distinguished from the motor fibers; the former could usually be traced for long distances in one direction, branches being given off at relatively long intervals, often at right angles. When the nerve fibers reach the transition zone between muscle fibers and tendon, they send off branches at quite regular intervals, which may, after a short course, lose their medullary sheath, and terminate in the ending or may divide into secondary and tertiary branches before losing the medullary sheath, each branch presenting its own ending. The end-apparatus is described as follows: The axis cylinder, after losing its medullary sheath, divides into two, three or four branches; each of these branches gives off in various directions numerous other fibrils, which again divide into branches of utmost fineness, which anastomose and intertwine forming a network with irregular meshes, at the nodal points of which thickenings are found. Such an end-apparatus measures 60-110 μ in length and 40-50 μ in breadth and is not only spread out over the surface of the tendon, but extends to some depth embracing several tendon fasciculi. Oval nuclei were now and then found on the fibrils of the network, especially on the primary branches.

The endings found in the tendons of the frog were essentially as above described for the lizard, except that the end-ap-

paratus was somewhat larger and its fibrils finer. The endings in the lizard and frog are not surrounded by a special sheath, being distinguished in this respect from endings found in birds and mammals. (*Vide infra*).

In the tendons of man and other mammals Golgi found two distinct types of end-organs. The one type, which resembles closely the corpuscles found in the conjunctiva and glands, will here receive no further mention, as they are foreign to the present contribution.

The other type to which he gives the name nervous musculo-tendinous end-organs ("*nervöse musculo-tendinöse Endorgane*") is deserving of further consideration.

This organ is of spindle form and varies in size from such as are 70-80 μ broad and 300-400 μ long to such as have a diameter of 100-120 μ and a length of 800 μ or even longer. One end of the spindle is always attached to a muscle bundle, while the other, which may be unbranched or double, becomes continuous with tendon fasciculi.

The line of demarcation between spindle and surrounding tendon fasciculi is usually quite distinct, the boundary of the spindle being often marked by a glistening line, along which nuclei are seen. The presence of a capsule does not seem indicated by this glistening line, although in silver nitrate preparations it would appear that there was present a superficial endothelial covering.

Golgi states that often only one medullated nerve goes to a spindle: not seldom, however, spindles to which two, three or four medullated nerve fibers go, may be seen. The medullated fibers, after entering the spindle, divide into primary, secondary and tertiary branches, these still retaining their medullary sheaths and diverging as they approach the periphery of the spindle. After the medullated branches have lost their myelin, they divide into several diverging branches. Golgi's account of the ending of these non-medullated branches is as follows: "*Wenn sie da angekommen sind*" (when the non-medullated branches reach the periphery of the spindle) "*bilden sie durch noch feinere und häufigere Zertheilungen in kurzen*

Zwischenräumen zahlreiche umschriebene, längliche, netzartige Geflechte, welche der Oberfläche parallel liegen." He draws especial attention to the similarity in the structure of the nerve endings found in the tendons of man and other mammals and those found in lizards, and to the resemblance of the nerve ending in tendon to that observed in the muscle plates.

Golgi found the "musculo-tendinous end-organs" very widely distributed, "if not in all, yet in nearly all muscles of the body," the eye-muscles forming an exception. He stated that they are most easily found in the rabbit, in which animal they are more numerous in the posterior than in the anterior extremity, being especially numerous in the deep tendinous lamina of the gastrocnemius and in the deep tendinous expansion of the back muscles. Similar observations were made in the mouse, dog and cat; in these animals, however, the endings are more difficult to find. In the bird, the greatest number of these end-organs was found in the wings and in the deep tendinous expansion of the large thoracic muscles.

Victor Marchi, soon after the appearance of the above communication of Golgi, investigated the tendons of the extrinsic eye-muscles with reference to the presence or absence of terminal end-organs in them. The Golgi tendon spindles were found by him in the tendons of the eye-muscles of cattle, swine, dogs, cats, rabbits and men. These observations were of especial interest in so far as they showed the presence of the nerve endings in the tendons of the eye-muscles, denied by Golgi. They added, however, little to the then existing knowledge of the manner of termination of the nerve fibers known to terminate therein.

In 1888, appeared a communication from Pansini on the nerve endings in the tendons of vertebrates. In his investigations he made use of the method suggested by Paladino, which consists in immersing small pieces of tissue, previously macerated in formic or arsenic acid, in a weak solution of palladium chloride; afterward he fixes the tissue in sodium or potassium iodide and teases and mounts the preparations in acidulated glycerine. By means of this method Pansini studied the nerve

endings in the tendons of the hippocamp (sea horse), torpedo, frog, lizard, tortoise, bird and mammal.

In the hippocamp he finds free endings, composed of branched or unbranched axis cylinders, having many small nuclei, some of these being mere granules and others large, round or oval nuclei. According to the number of nuclei, the length of the pedicles and the length of the axis cylinders, the whole plaque resembles a bush, a tuft, or rarely a star-like small plaque. Pansini considers these morphologically equivalent to motor endings.

For the torpedo, he describes a rich plexus with large, irregular meshes, in which are found plaques consisting of medullated fibers, which branch and rebranch and finally become non-medullated and have many round or oval nuclei attached, some small and granular, others larger and having nucleoli. Three classes of endings are described—one free; one larger and surrounded by a thin membrane; the third surrounded by a definite capsule.

In the frog and lizard, he used the tendo Achillis and the tendons of the small muscles of the foot. The nerve ending consists of a fine delicate reticulum at the nodal points of which are granular nuclei, some showing nucleoli. The endings are free in the frog and generally in the lizard, but in some cases in the lizard, the sheath of Henle of the nerve innervating the organ forms a sort of investing capsule. In the lizard, also, the network is more complicated, the plaques larger and the nuclei more numerous, with more of those that have nucleoli. In the tendo Achillis of the turtle are found the beginnings of true neuro-tendinous organs of Golgi. Two to five plaques like those described for the frog and the lizard, are grouped into a quite definite organ, surrounded by one or several layers of connective tissue—elementary neuro tendinous organs. These plaques are arranged on tendon fasciculi, whose elements are smaller and more numerous than those of the surrounding tendon. The fusiform enlargements found in connection with the nerves supplying tendon, and mentioned by Golgi, Cattaneo and Mar-

chi are considered by the author as nerve endings like those of Pacini and Krause, but less developed.

In the aponeurosis of the pectoral muscles of the dove, he finds neuro-tendinous end-organs more numerous and more elongated than in the turtle, but containing plaques similar to those described above.

In mammalia (dog, rabbit and man), the plaques are the same as in the lizard, but the nuclei are larger, more granular and more abundant and more plaques are grouped together within one connective tissue sheath to form the neuro-tendinous organ.

Opposing the idea of Golgi that these organs are always muscular at one extremity and tendinous at the other, which gave to them the name "musculo-tendinous end-organs," Pansini states that he has found neuro-tendinous end-organs frequently, in mammalia as well as in the lower vertebrates, which were tendinous at both extremities. Besides these organs, he also finds in tendon, corpuscles resembling those of Pacini, Meissner and Krause. From Pansini's descriptions and from his figures, compared with the corresponding figures of Ciaccio and with our own, we are led to conclude that in his preparations, the ultimate terminations of the non-medullated fibers were very imperfectly stained.

Contemporaneously with Pansini, Cattaneo published the results of his investigations with the double chloride of gold method, applied to tissues previously made transparent by immersion in arsenic acid and fixed in osmic acid. His studies were confined to neuro-tendinous end-organs of guinea pigs, rabbits, cats and dogs. Cattaneo's minute description of the general structure of the organ does not differ materially from that given by Golgi. He demonstrates, however, a distinct capsule for the spindle, consisting of one or several layers of fine, interlacing connective tissue fibers, which, in his silver nitrate preparations, are seen to be covered by a layer of large, polygonal endothelial cells with round or oval nuclei, resembling those described by Ranvier for the sheath of Henle; the author concludes from this, that the sheath of Henle of the

nerve fiber terminating in the spindle constitutes the investment.

Cattaneo also mentions a collar or ring, surrounding one extremity of the spindle, which, he thinks, may be due to the action of the acids, or may consist of circular or spiral fibers surrounding the spindle or may be regarded as the termination of the capsule.

He emphasizes the fact that the spindles vary with the age of the animal, being smaller, less prominent and with more numerous nuclei in the young than in the adult of the same species; also that they vary with the species, being smaller and less distinct in the guinea pig than in the rabbit, while in the dog, the spindles are still larger, approaching those of man, in whom are found very large and complicated end-organs.

The nervous structure he describes as follows: Generally but one nerve fiber innervates the organ, rarely two; oftener one fiber divides and supplies two or more organs. This nerve fiber generally divides before entering the spindle, loses its sheath of Henle as it enters, which becomes continuous with the investing capsule; these medullated fibers then divide and redivide, always approaching the periphery of the spindle, either suddenly or gradually becoming non-medullated. Finally the pale fibers reach the periphery, where, by finer and closer ramifications, they form numerous, circumscribed reticular networks, like small tufts, sometimes well isolated, sometimes closely crowded together, which cease at some distance from the periphery. "These networks" he says, "show from time to time nodosities which may be due to the action of the arsenic acid on the nerve termination."

The blood supply of these organs comes from the neighboring vessels, which send generally two, but sometimes only one branch to supply the spindle. These run along on either side of the spindle and send off side branches at intervals which anastomose with those from the opposite side, thus forming a long-meshed plexus somewhat resembling that of muscle.

The author discusses at some length the relation of these organs to other sensory corpuscles, such as neuro-muscular spindles, Pacinian corpuscles, corpuscles of Krause, etc., de-

ciding that, while these different forms of nerve endings are often found very near together and while he even occasionally finds Pacinian corpuscles incorporated in the substance of the tendon spindle, yet the nerve supply is always distinct and he believes that the relation is accidental.

In order to decide the question of the function of the neuro-tendinous spindles, Cattaneo undertook a brief series of degeneration experiments. In the first set of experiments, he sectioned the posterior roots, causing an ataxic gait, but no degeneration of the neuro-tendinous spindles was found and he considered these experiments as negative.

In the second set, he sectioned the anterior roots, causing paralysis of the posterior extremities and degeneration of the muscle fibers and nerves supplying them, while the neuro-tendinous spindles and their nerves were unaltered. In the third set of experiments he sectioned the sciatic nerves and found that the intrafusal tendon fibers were reduced in size and otherwise altered, a long time after the operation, while the nerve supplying the spindle showed the usual degeneration phenomena soon after section of the nerve, the termination of the non-medullated fibers in the spindle being still more radically and quickly altered. From these facts and from their position in the boundary zone between muscle and tendon, the author concludes that these organs are sensory and probably organs of muscle sense.

Apropos of Cattaneo's degeneration experiments, it may not be amiss to mention briefly Brazzola's investigations on *tabes dorsalis*, in which he examined for pathological lesions, not only the central nervous system, but also some peripheral nerve endings—among them the neuro-tendinous end-organs. He finds the ultimate portion of the nerve fiber going to the plaque altered and also the ramifications of the axis cylinder. Only the "bush-like terminations in ring or spiral" of Ciaccio remain, very much atrophied and these too finally disappear.

In the fifth edition of his *Handbuch der Gewebelehre*, Kölliker mentions having observed nerves in the tendons of the bat. The details concerning their mode of ending seem, how-

ever, to have escaped this observer at that time. In the sixth edition of this well known work, Kölliker considers these endings much more fully. His later observations may be summarized as follows: He corroborates Golgi's statement that in lizards the nerves terminating in tendon end in a dense network of non-medullated nerve branches, with here and there free endings and occasional enlargements, but adds that "*diese sensiblen Endplatten*," as he terms these endings, consist, as do the motor endings, of non-medullated fibers, surrounded by a nucleated sheath of Schwann. Concerning the "*Golgi'schen Sehnenspindeln*" as he terms the "*Organi nervosi terminali musculo-tendinei*," in honor of their discoverer, he makes the following comment: In one individual seven years old, the Golgi tendon spindles were 1.28 mm. to 1.42 mm. long and 0.17 mm. to 0.25 mm. broad at the muscular end. In the rabbit, they were 0.24 mm. to 0.79 mm. long and 0.02 mm. to 0.11 mm. broad. The Golgi tendon spindles are surrounded by a well developed fibrous tissue capsule, which is continuous with the sheaths of the contiguous tendon fasciculi. This capsule, he believes with Cattaneo, possesses an endothelial lining. Within the capsule, there are found two, three, and sometimes more tendon fasciculi, at other times, as it would seem, a less differentiated mass of tendon substance (*eine mehr zusammenhängende Masse von Sehnensubstanz*). One, two, three or four medium sized medullated nerves go to each spindle, which they reach, usually in the equatorial region, but not infrequently at one end of the spindle. These nerves divide into a number of medullated branches and are distributed through their non-medullated terminal branches, over the greater part of the thicker portion of the spindle. Kölliker's observations on the ultimate ending of the spindle nerves are in accord with those given by Golgi and Cattaneo and will therefore need no farther mention.

In a summary of observations on sensory nerve endings, Kerschner mentions briefly his own observations and those of other investigators on the nerve endings in tendon, giving, however, no figures to elucidate his text. In amphibia, he was not able to add to the results obtained by Rollet and Gemt. The

end-organs obtained by Golgi, he regards as modifications of Rollet's "*Endschollen*," to be distinguished from the latter largely by the fact that they are partially separated from the contiguous tendon fasciculi by a sheath lined by endothelium which he regards as a continuation of Henle's sheath of the nerve terminating in the end-organ. Kerschner regards the term "*organi musculo-tendinei*" as inappropriate, as these structures are not always found near the muscular end of the tendon. The tendon nerves, Kerschner states, do not end, as Golgi and Cattaneo had stated, in a network of anastomosing terminal fibrils, but in freely dividing and intercrossing branches, which do not anastomose and often terminate in end-knobs, which now and then appear to be in connection with cells found by him within the end-organs.

In 1888, 1889 and 1891, articles appeared from the pen of Ciaccio, describing the results of his investigations with the double chloride of gold method of Fischer and Löwit on the nerve endings in tendons of mammalia, birds, reptilia, amphibia and fish. His researches are the most exhaustive and his diagrams and descriptions are the most accurate and minute that have appeared up to the present time, especially since, by means of longitudinal and transverse sections of the tendon corpuscle, he has observed and pictured the minute internal structure of the organ, the details of the nerve ending and its relation to the intrafusal tendon fibers in a way which is impossible from mere surface preparations. For these reasons we desire to give a somewhat more extended account of this author's work.

He finds these nerve plaques (either encapsulated or not) which he designates "*plaques tendineuses avec terminaison buissonneuse des nerfs à anneaux ou à spirale*," in the tendons of all vertebrates studied except the *Batraciens anoures* (frog, toad and tree-toad), in which the nerve ending is free on the primary tendon bundles and is of such form that he designates it "*buisson nerveux final*."

Ciaccio describes three peculiarities of the neuro-tendinous organs of mammalia, not noticed by previous writers: (1) spin-

dles, found in the eye-muscles of man, in which both extremities are tendinous; (2) compound spindles, united together along their whole length, but each part having an independent nerve supply; (3) neuro-tendinous end-organs into which some of the muscle fibers are prolonged into the organ to the margin and even to the middle of the nerve plaque.

His description of the nerve ending is as follows: The numerous ramifications of the axis cylinders, which compose the nerve plaque in the neuro-tendinous end-organ show along their course certain enlargements of different form and size, described by most writers as nuclei, but really, he believes, masses of one of the two substances of which the axis cylinder is composed (neuroplasm). Most of these ramifications are plates with one or several transverse projections or "crêtes d'empreinte." These ramifications are arranged in different planes, thus producing the plexus-like appearance described by Golgi and others who viewed the corpuscles only in surface preparations. Sections—cross and longitudinal—showed that "the branches of the axis cylinder run across the loose connective tissue which binds the primary tendon bundles together, then penetrate these latter and continue to ramify in a bush-like manner; each branch surrounds in spiral or ring, in several parts of their length, one or several of the small bundles of dense fibrillar connective tissue of which each primary tendon bundle is composed."

This description of nerve ending applies also to the ending of the nerves in the neuro-tendinous end-organs of birds.

In reptilia, however, in which he has studied the tendons of the interspinous muscles of the *Coluber natrix* and of the gastrocnemius of the *Lacerta agilis*, no encapsulated organs are found. The nerve plaques are distributed along the medullated nerves which divide repeatedly and end in the depths of the tendon in a confused intercrossing of very fine fibers, thread-like or ribbon-like, beset with projections of different form and size. These fibers also surround the primary tendon bundles in ring or spiral before their final termination.

In amphibia, however, he finds no plaque as above de-

scribed, but a plexus of fine fibers which end in a bush-like expansion of small varicose nerves ("*touffe nerveuse finale*") of which the greater number penetrate the primary tendon group and probably end free without surrounding the bundles.

In the fish, which only he and Pansini have studied, he has examined the tail and fin tendons of the ray, the tench and the carassin. He finds medullated nerves ending free, more or less deeply in the tendon, in peculiar plaques, simple or compound, formed of axis cylinders in the form of turns of ribbon ending in a "*ligne en relief*" or "*crete d'empreinte*," which is more deeply stained in gold chloride than the rest of the ending. Each turn of the ribbon corresponds to a turn of the axis cylinder which surrounds one or several of the small secondary tendon bundles.

Concerning the function of the neuro-tendinous end-organs, the author considers the sensory nature proven both by the microscopic anatomy and by physiological experiment. The special function being, however, still unsettled, the author advances the view that it is "to proportion the amount of distension and resistance of the tendon to the amount of contraction of the corresponding muscle," supporting his view by the fact that the most frequent site of these organs is in the tendons of the most active and efficient muscles.

In 1890, Mazzoni described and figured certain forms of terminal nerve organs found in the tendons of man. Similar organs had been mentioned by Golgi and Ciaccio and were afterwards noted by Ruffini, the two latter finding them in the tendons of other mammalia than man. These are often found in more or less intimate connection with the neuro-tendinous end-organs and may therefore be mentioned in this connection. In their simplest form, where a single nerve fiber enters and passes unbranched through the encapsulated granular substance, ending in a terminal enlargement, they closely resemble small Pacinian corpuscles. In the more complicated forms, however, where a single branched nerve or several independent nerves enter the granular substance and break up into many branches, forming a twisted, network-like mass, each filament ending in a

terminal enlargement, the resemblance to the Pacinian corpuscles is lost and it is to these especially that the name "Golgi-Mazzoni organs" is sometimes applied.

In 1893, Ruffini, in a brief note, described the results of some investigations, by means of Fischer's gold chloride method, on the neuro-tendinous end-organs of the cat.

In this communication, waiving the questions of the structure of the organ and the form and relations of the nerve ending therein, he emphasizes the fact, already discovered by Cattaneo, that Pacinian corpuscles are found, not only near the neuro-tendinous end-organs, but even within their capsules. In two later communications, of which we have seen only the reviews, he again dwells upon this relation, which he, disagreeing with Cattaneo, considers important in the consideration of the structure of the neuro-tendinous end-organs of the cat. He says that in this animal, from one to five Pacinian corpuscles are found in each neuro-tendinous end-organ. In the rabbit, although they are found, there are not so many nor is the relation so close.

He also, in all these communications, describes a reticulum ("*réticule nerveux*") which is sometimes found on the neuro-tendinous end-organs of the cat.

The nerve fiber forming this network may be a branch of the nerve supplying the tendon organ or may be independent of it. This nerve becomes non-medullated, divides and subdivides, the resultant branches twining themselves about the neuro-tendinous end-organs, not anastomosing, and finally ending in a small ball-like enlargement on the striated muscle, either near the neuro-tendinous organ or at some distance from it.

The author speaks also of the "*bandelette*" of connective or elastic tissue surrounding the organ at one of its extremities and mentioned by Cattaneo and Ciaccio. In none of these communications, has Ruffini added anything to our knowledge of the structure and nerve terminations of the end-organ.

In a recent article, Ruffini describes a new nerve ending found in the sub-cutaneous connective tissue of the human

finger. He used Fischer's gold chloride method upon material taken from the fingers of a girl of eleven years. The ending is spindle-shaped and consists of bundles of white fibrous and yellow elastic connective tissue fibers surrounded by a capsule largely of yellow elastic tissue. The author thus distinguishes this spindle, which may bear his name, from the neuro-tendinous end-organs of Golgi.

(1) In the neuro-tendinous organ, the medullated fiber runs a nearly straight course to the point where it becomes non-medullated, while in the Ruffini spindle, the nerve makes long and tortuous turns in the interior of the spindle before becoming non-medullated.

(2) In the neuro-tendinous organ, the non-medullated nerve breaks up rapidly into short, ribbon-like branches in the form of arborizations, while in the Ruffini organ, the divisions are irregular and the branches long, tortuous and varicose.

(3) The plaque-like distribution met in the neuro-tendinous organ is never found in the author's spindle.

(4) The Golgi organs, in transverse section, show a rather regular arrangement of the turns of non-medullated fibers in spiral or in ring around the small tendons of the organ, the intertwinings never completely occupying the cross section. In the Ruffini organ, the twinings are very regular and occupy the whole cross section, so that nearly all the serial sections show about the same figure.

(5) The Ruffini organ is composed of connective and elastic tissue, while the Golgi organ consists of tendon fasciculi.

We have given somewhat fully Ruffini's account of the nerve end-organ found by him in the connective tissue of the hand, since by doing so, we have been able to give, in an indirect way, Ruffini's observations on the terminations of nerves in the neuro-tendinous end-organs.

In 1893, Smirnow published some observations on the terminations of nerves in the frog and toad, having used a modification of Ehrlich's *intra-vitam* methylen-blue method. He finds, in the musculus sterno-radialis and musculus semi-tendinosus, special tendon nerves and nerve endings which extend to

the muscular extremity of the tendon. These tendon nerves, in the frog and toad, end in the shape of groups of tufts of fine varicose fibrillae, situated between the tendon fibers. The number of tufts depends on the number of medullated fibers entering the tendon, this in turn depending on the size of the animal and therefore the size of the tendon. These nerve endings are situated at different depths in the tendon. His figures agree in the main with those given by us.

In the same year, appeared a communication from Ivanhoff, in which among nerve endings in other connective tissues, he describes the sensory nerve endings in the fascia lumbo-dorsalis and fascia transversalis and the fascias of the anterior and posterior extremities of the rabbit, cat and dog. The method used by Ivanhoff also, was the *intra-vitam* methylen-blue method of Ehrlich. He describes three types of endings: (1) those in the form of a tassel; (2) some in the form of a bush; and (3) others in globular form. The terminal filaments may end abruptly or in an enlargement or in a more or less complicated ending resembling a snare. These endings have no capsule and are identical, according to Ivanhoff, with the nerve endings in tendon. While some of the figures given by Ivanhoff resemble somewhat the nerve plaques found in the simpler tendon end-organs, we do not think, either from his description or his figures, that these endings can be considered identical with the endings found in the neuro-tendinous end-organs of the animals he has studied.

In turning now to our own observations, we may again call attention to the methods used by us. As may have been observed, all investigators, with the exception of Smirnow and Ivanhoff, who have studied nerve end-organs in tendon, have employed one or the other of the gold chloride methods, or platinum chloride, for staining the nerve terminations. And while it is not our purpose to reflect in any way on the results obtained with these methods, and while we are ready to accord all observers who have used them due credit for the many valuable observations which they have made, we can but feel that the methylen-blue method, as used by us, and especially in the

end-organs under discussion, gives results which should be given consideration whenever they are at variance with the results obtained by the older methods.

We shall discuss our own observations *seriatim*, beginning with the amphibia.

Amphibia.

Of the results obtained by numerous observers who have studied the terminations of nerves in the tendons of amphibia, those obtained by Ciaccio and Smirnow were such that we find it unnecessary to add materially to the account given by them. A corroborative statement may, however, not be wanting in value.

Rollet, who first described the termination of nerves in the tendon of the frog, designates the endings in them as "*Nervenschollen*" and finds two parts, the one consisting of a short internodal segment, ending in a sharp point, the other of small cellular plates with round nuclei or of grains arranged in undulating lines and separated by spaces of the same form. Sachs and Gemt described non-medullated fibers in the endings; Golgi described a network of small non-medullated fibers; this Kölliker corroborated, adding that the nerve branches of the ending were invested with a nucleated sheath of Schwann. Ciaccio, after describing the arrangement of the nerve in plexus, says that it ends in a peculiar nerve plaque which he designates as "*touffe nerveuse finale*." These tufts, he says, are oblong in shape, larger in the middle than at the extremities, and composed of a bush-like mass of fine varicose fibers, which penetrate the primary tendon groups and end in free endings. He thus disagrees with Gemt and Golgi, who affirm that the nerve ending in the frog is the same as in reptilia.

Smirnow also describes nerves ending in tufts of fine varicose fibrillæ, situated between the tendon fibers. The figures given by Smirnow, who, it may be remembered, used the methylen-blue method in his investigations, are very similar to the ones we give for the nerve ending in the tendon of the frog, although it would appear to us that our endings were more fully stained or that we were dealing with much larger endings.

In the frog, in many thin, flat, fascia-like tendons, into which the muscle fibers are inserted, notably in the tendon of the *tibialis posticus* from which many of our preparations were taken, we have found numerous terminal arborizations of nerve fibers.

Often we have been able to trace medullated nerve fibers for some distance, which, at each node of Ranvier, send off a medullated branch, which passes out for a considerable but variable distance from the parent trunk and then breaks up into a large number of fine non-medullated nerves, all extending in the same general direction and sometimes branching again and appearing as ordinary varicose fibers. The varicosities are all round or oval in shape, vary but little in size and are connected by very fine thread-like fibrillæ. There are usually no side branches and no projections along the course of the non-medullated nerves, but the nerve fibers differ in length and the whole tuft looks not unlike a small tree-like bush with long, slender nearly parallel branches, tapering toward the top, on which the buds are somewhat swollen, but which are unadorned with flowers, fruit or foliage.

Occasionally at the end of some of the terminal branches, may be seen a round or oval enlargement somewhat larger than the varicosities found along the non-medullated fiber. At other times, the fiber seems to stop quite abruptly as if it were broken off, or it may terminate in a sharp point. This description of terminal nerve tufts applies equally well to all the plaques seen in the frog. Whatever variation is seen in the ending is due therefore to the arrangement of these plaques and their relation to each other and to the medullated nerve. At times, the medullated nerve divides into two main branches at right angles to the stem, each of which quickly breaks up into a tuft similar to the one just described. The whole appearance is then not unlike what might be presented were two such bushes as above described, cut off just below the point of branching and placed base to base. Occasionally we see a tuft from one nerve fiber extending out and meeting one from another nerve fiber, the whole forming a spindle-shaped ending with medullated fibers

at each extremity such as may be seen in the central tuft of Fig. 1, Plate XIII.

Sometimes a nerve fiber approaches an end-tuft from a direction at right angles to its length ; but before reaching it, divides into three or four branches, each of which ends in a typical end-bush, but all so massed and mingled together as to produce a most complex picture. At other times, the main nerve, as it nears its extremity, shows very short internodal segments, and at each of the nodes, a short medullated nerve, branching and rebranching and ending in a typical tuft, is given off, the whole producing the effect of one very large ending, spread out over a considerable space. In Plate XIII, Fig. 2, we have represented such an ending, in which the main nerve divides into seven or eight branches, each subdividing a number of times, and each subdivision terminating in a tuft of varicose fibrils and producing the tree-like ending seen in the figure, with its large bushy spreading top. In Plate XIII, Fig. 1, we have represented a very large ending, arising from the terminal branching of a large medullated fiber. This fiber first divides into two branches, one of which soon redivides into two secondary branches, at right angles to the main stem, which soon end in the tuft of varicose fibrils. The other primary branch extends for some distance before dividing into two secondary branches, one of which divides into tertiary branches at right angles to itself and all terminate in end-tufts. One of the latter tufts passes back and meets the top of the tuft coming from the first branch, forming the spindle-like ending seen in the center of the figure and previously described. We have found endings of the most varied size and complexity, depending on the number of branches given off at each division and entering into the formation of the end-organ. It has not been unusual to observe twelve to fifteen end-tufts of different size and shape, formed by the division of a single nerve fiber.

Longitudinal sections of the frog's tendon, as represented in Plate XIII, Fig. 3, show that these end-brushes are found, not in the zone of passage from muscle to tendon, but deeply embedded in the tendon. They show also that these endings

are spread out on peculiar bundles of tendon fasciculi, which are sharply differentiated from the surrounding tendon fasciculi by reason of the fact that they are smaller, stain much more deeply with alum carmine and show large numbers of round, oval or oblong nuclei, which also stain deeply red in alum carmine, even in preparations in which the ordinary tendon nuclei are not at all stained. The tendon on which the nerve ending is found partakes, in other words, of the character of embryonic tendon. We see also in longitudinal sections that the varicose fibers described either lie on the surface of the tendon fasciculi in long, undulating lines, or twine about or between them in long serpentine windings, while the cross sections show especially well that the fibers penetrate these fasciculi and terminate, usually with no enlargement, on the smaller bundles of which the primary fasciculi are composed. We see also in cross sections, as in Plate XIII, Fig. 4, that, sharply as the tendon bundles are differentiated from surrounding tendon and compact and complicated as the whole ending often appears, there seems to us to be no indication of a connective tissue capsule surrounding the fasciculi and holding them together. The nerve ending in frog's tendon is, as has been stated by Cattaneo, Ciaccio, Smirnow and others, a free ending.

As stated in the introduction, many of our preparations, after staining in methylen-blue, were fixed in ammonium picrate and cleared, teased and mounted in glycerine ammonium picrate. This fixative softens somewhat the tendon and connective tissue and the whole ending is readily flattened out. While this, it seems to us, is an advantage in studying the final terminations of the nerve fibers, their size, shape and relation to the main nerve fibers, yet it sometimes gives a rather false idea of the end-organ and the relation of the nerve ending to the tendon fasciculi of the organ, unless this idea is corrected by comparison with preparations fixed in ammonium molybdate and either cleared and teased in xylol and mounted in balsam, or sectioned longitudinally. This fact can be readily substantiated by a comparison of Figs. 1 and 2 of Plate XIII, which are surface preparations, teased out of the glycerine-ammonium picrate

solution, with Fig. 4 of Plate XIII. which gives more nearly the natural size of the organ.

Reptilia.

Our own observations on the termination of nerves in the neuro-tendinous organs in reptilia agree more closely with those made by Ciaccio than with those recorded by Golgi and Panzini, who described a network of fine nerve branches, at the nodal points of which thickenings are found. Ciaccio investigated under reptilia the tendons of the interspinous muscles of *Coluber natrix* and the tendon of the gastrocnemius of *Lacerta agilis*. He found in these no true Golgi neuro-tendinous end-organs, but nerve plaques situated in small tendinous groups, primary as well as secondary. "The plaques," he says, "consist of a confused intercrossing of very fine fibers, some filamentous and some ribbon-like, arranged in two planes and beset with projections of different form and size." In cross sections, he showed that the fibers, near their termination, penetrate the primary tendon bundle and surround one or several of the secondary tendon bundles composing it. In our investigations, we have used almost exclusively the tendons of the posterior extremity of *Emys melcagaris*, especially the flat tendinous aponeuroses of the quadriceps extensor and the tendon of the gastrocnemius. In this animal as in the frog, we have frequently been able to trace large medullated nerves with rather short internodal segments, for considerable distances, which, at each node of Ranvier, give off a medullated branch and sometimes more than one. This, after a longer or shorter course, terminates in a more or less complex end-arborization. In some cases the medullated nerve divides into four or five finer medullated nerves, some of which break up at once into a number of non-medullated fibers; others extend for considerable distances along the tendon and toward its extremities, giving off at intervals side branches, which either are or soon become non-medullated or divide into numerous non-medullated nerves. Thus, along such an ending, very large numbers of such tufts may be seen. After losing the medullary sheath, the fibers

proceed for a variable distance along the tendon fasciculi, some as simple varicose fibrils, like those described for the frog, but most of them beset by round, oval, or oftener very irregular enlargements, either resting directly on the fiber or supported by a longer or shorter pedicle. These enlargements, which so sharply distinguish this end-plaque from that of the frog, vary markedly in size and form. Sometimes a fine branch serves as a pedicle for one or several granular enlargements, pear shaped, irregularly quadrangular or polygonal or leaf-like or resembling a large plate beset on several sides by sharp thorns or triangular or quadrangular or oval bud-like projections. Sometimes the non-medullated nerve fiber itself enlarges and is beset with secondary enlargements of the most varied size and shape. Sometimes a single enlargement rests on a rather long stem; at other times, the pedicle itself is adorned with other sessile or pedunculated enlargements, or may divide at its extremity into two or three branches, each supporting one or more of the enlargements. Thus the plaque may be quite simple or much more complex. Sometimes the nerve enters the ending, the branches with their terminal tufts spreading in opposite directions. Sometimes it enters at one extremity, all the branches extending in the same direction, more closely resembling a bush whose branches are adorned with the most fantastic foliage. Sometimes the main nerve fiber breaks up near its extremity into a large number of fine branches, coming off at different closely approximated nodes, each branching repeatedly and ending in the characteristic end-plaque, the whole somewhat resembling in general appearance, though not in the minuter structure, the large, bushy ending described and figured for the frog.

In Plate XIV, Fig. 5, we have represented one of the simpler endings, which has been very much flattened out, so that the form and relative size of the final tufts and their relation to the nerve fiber are very well shown, with no attempt to represent the relation to the tendon fasciculi. The medullated nerve sends off two medullated branches from neighboring nodes, each ending in a short, simple tuft. The nerve finally

divides dichotomously, one of the resultant branches terminating quickly, while the other gives rise to two sets of tufts, before breaking up into its final arborization.

Longitudinal sections, as represented in Plate XIV, Figs. 7 and 8, show that in the turtle, as in the frog, the tendons on which these nerve endings are arranged, have not the characteristics of ordinary tendon, but have smaller tendon fasciculi and many more nuclei, both fasciculi and nuclei staining more deeply than the surrounding tendon. The endings are usually found deeply embedded in the tendon and may even be nearer its superficial surface than its muscular face. In some cases, however, as in Plate XIV, Fig. 7, they are found just at the boundary of muscle and tendon. We see also that the terminal fibers have a somewhat undulating, serpentine course, winding about or between the tendon fasciculi, while the terminal plates may enclasp or partially surround the smaller bundles of tendon fibers. Neither the spirals nor the rings, however, which are so strongly emphasized by Ciaccio in both his figures and his descriptions as a most characteristic feature of the terminal plaque, seem, in our preparations and figures, so definite and strongly marked a feature of the ending as his figures would seem to indicate. This fact, which we note in all our preparations from all species of vertebrates studied, may, it seems to us, be due to the fact that, while the gold chloride stains, not only nerve fibers, but also tendon fasciculi, connective tissue, tendon cells and nuclei, or may precipitate in the lymph spaces or semi-fluid ground substance, so that the appearance is often deceptive, the methylen-blue far more sharply differentiates the nerve structures from all other tissue elements of the end-organ. In many preparations which we believe to have been perfectly stained and in which only the nerve fibers and their terminal ramifications were blue, we have found no rings, such as Ciaccio finds in all his preparations, except those from the amphibia, and no spirals, the rings being reduced to a clamp-like partial encircling of the tendon by the terminal disks, and the spiral to an occasional loose winding of the fine terminal fibers in and out between the bundles of tendon.

In cross sections, as represented in Plate XIV, Figs. 9, 10 and 11, we note the small size of the tendon fasciculi and the large number of nuclei and that the non-medullated nerve fibers penetrate the tendon fasciculi, while the terminal plate-like enlargements are found clasping one or more of the smaller bundles of connective tissue fibers of which the fasciculi are composed.

Golgi and Ciaccio, from the various reptilia which they examined, concluded that in this type of vertebrates, as in the amphibia, the nerve endings were free and that no encapsulated endings were found, as in the higher vertebrates. Pansini, however, while he finds the endings in the lizard either free or surrounded by an imperfect sheath, finds in the turtle the beginning of true Golgi neuro-tendinous organs, surrounded by a distinct capsule of connective tissue. In the majority of our preparations, the absence of a connective tissue sheath is easily noted, the peculiar tendon fasciculi, on which the nerve ends, fading off gradually into the ordinary tendon. But in some of our preparations, we have been able to demonstrate a more or less distinct capsule of connective tissue fibers, surrounding a spindle-shaped group of fasciculi, on which a more or less complex nerve ending was found. This capsule has been especially well shown in transverse sections of the tendon, one of which is shown in Plate XIV, Fig. 11. It may be added that we have usually found the encapsulated organs in the zone of passage from muscle to tendon, while the non-encapsulated or free endings were found deeper in the tendon and showing no relation to the muscle. There seems, however, to be no particular tendon or part of the body in which encapsulated forms are especially prevalent, but they are often found in the same tendon with non-capsulated endings. The nerve endings in the encapsulated forms seem generally more complex than those in the free ending.

Bird.

Golgi and Pansini describe, for the bird, endings like those which they described for the lizard—networks of fine fibers at the nodal points of which thickenings or nuclei are found. Our

results, however, are more in accord with those of Ciaccio, who, investigating with the gold chloride method the nerve endings in the tendons of the wing muscles of the sparrow, the sparrow and the swallow, found the nerve plaques always in the neuro-tendinous end-organs of Golgi, surrounded by a connective tissue sheath and an endothelial investment. He finds that usually only one nerve fiber innervates the organ; this may divide, either before or after entering, into two primary branches each passing toward an opposite extremity of the organ. They divide and subdivide into many non-medullated nerves, which form the plaques, appearing as a multitude of small pieces of axis cylinders, differently formed and grouped in masses ("groupés en amas"). His cross sections show that the nerves pass between the small bundles of fibrillar connective tissue of which the tendon fasciculi are composed, embracing one or several of them before ending.

Ciaccio's results regarding the general structure of the organ in birds have been in most particulars corroborated by our observations with the *intra-vitam* methylen-blue method, on the tendons of the wing muscles of doves. Although in most cases the ending has been surrounded by a distinct investment of connective tissue and endothelium, we have been able to see endings, which like most of those in the turtle, possessed no capsule, but were distributed free on the primary or secondary tendon groups. While the usual encapsulated form was always found at the musculo-tendinous junction, these free endings were usually found embedded somewhat more deeply in the tendinous tissue. In these, however, as well as in the encapsulated forms, the tendon fasciculi differed from the ordinary tendon fasciculi in the same way as has been described for the frog and the turtle, staining more deeply and possessing more numerous and more deeply staining nuclei.

The form and size of the neuro-tendinous end-organs in birds vary according to the number of nerves which supply them and the part of the organ where the nerves pierce the capsule. Sometimes a medullated nerve passes along the muscle or tendon and, without changing its direction, branches into

two or three primary medullated branches, each of which sooner or later re-divides and ends in one or several non-medullated fibers. Side branches are also given off, which, after a very short course, divide into two or three non-medullated fibers, which usually run nearly parallel to the main nerve of the ending. In the bird, as in the turtle, the characteristic appearance of the end-tuft is produced by peculiar, fantastic enlargements, granular in appearance and of the most varied size and shape, which beset all the non-medullated fibers. Sometimes they are quite regularly round or oval, but oftener they are very irregular, plate-like, with prominent projections, which may be pointed, blunt or round, or they may resemble long leaves somewhat twisted. These enlargements are in general longer and more complex than those that we find in the turtle, the form which seems to predominate being that in which the non-medullated fiber itself enlarges, widens out into a large, irregular granular plate, other granular plates, round, oval, rectangular, club-shaped or spike-like, being added on, now at the side and now at the end, and still others, until we have a long, irregular string of such granular masses, at no point showing a return to the normal size of the non-medullated fiber.

The complexity of the ending may be varied by the number of times that the non-medullated fiber branches before thus spreading out into this terminal enlargement, and by the number, size and shape of the granular plates that are thus pieced on to the simple terminal enlargement. In addition to these widenings of the main stem, we have also numerous varicosities, which may rest directly on the main stem before its final enlargement, or may be separated from it by a slender pedicle.

The medullated nerves are usually quite straight throughout their length, but the non-medullated fibers wind in long, sinuous waves, now for some distance on the one surface of the tendon fasciculus, now partly surrounding it and now coiling from one fasciculus to another, finally entering one of the peripheral fasciculi and passing between the secondary bundles of tendon fibers composing it, while the side and terminal enlargements enclasp the bundles of tendon fibers, partly encircling

them. The fibers and terminations passing in the same general direction while the enlargements are long and generally slender, the side projections being rarely lifted far from the parent stem, gives a rather cylindrical shape to the entire ending, a form which we have not found unusual for the bird, although Ciaccio mentions that he has found it quite rare. In all the endings observed in the bird, we have found terminal plaques similar to those described above, but there are variations in the length of the terminal plaque and also in the number of plaques taking part in the formation of the neuro-tendinous end-organ. Sometimes the varicosities are so small and closely packed together and the fibril so straight that it resembles somewhat a sprig of mignonette, with its straight slender stem and small, closely packed pedicled flowers surrounding the stem on all sides. The length, thickness and compactness of the terminal plaque differ in the different end-organs and also their number and arrangement and hence the form of the entire end-organ.

Often one or several medullated nerves enter the organ, either at the extremity or in the equatorial region, breaking up near the center into three or four medullated fibers, which spread out, re-divide, become non-medullated, each branch terminating in the characteristic varicose end-plaques. Such a spindle is shown in Plate XV, Fig. 13. The spindle is rather short, broad at the center and tapering at the two extremities. Or we may have organs like that represented in Plate XV, Fig. 15, where the spindle broadens out at the center, tapering at one extremity, and, at the other, dividing into two parts into each of which the terminal plaques extend. In plate XV, Fig. 12, is represented a rather simple ending, which has been so flattened out that the one medullated nerve, with its two primary branches and their seven or eight terminal plaques are spread out all in nearly the same plane and their relation to the tendon fasciculi is not shown. In this end-organ, there was no capsule, or at most, a very imperfect one. While this preparation gives us no idea of the structure of the end-organ, it shows more clearly than any other preparation the character of the terminal plaque. In Plate XV, Fig. 14, is a rather simple end-

ing, consisting of one medullated nerve which branches little and shows only a few terminal plaques.

Longitudinal sections, stained in methylen-blue and counter-stained in alum carmine, as represented in Plate XV, Figs. 16 and 17, show that the few large tendon fasciculi, which enter the spindle, break up into smaller fasciculi and these still farther divide and then re-unite at the distal extremity of the spindle; that the intrafusal tendons have very numerous nuclei, oval or elliptical; that the non-medullated fibers have a sinuous course, now on and now between the tendon bundles, while the terminal plates are granular and seem to pass between the bundles of fibrillar connective tissue. In some cross sections, as shown in Plate XV, Figs. 18 and 19, we see a thin connective tissue capsule, which is seen to be wanting in others. We see also that the medullated nerves pass in the connective tissue surrounding the fasciculi while the non-medullated fibers, as Ciaccio has mentioned, penetrate the fasciculus and end on the small groups of fibrillar connective tissue of which the fasciculus is composed.

Mammalia.

Concerning the general structure of the neuro-tendinous end-organs in the different forms of mammalia studied, our observations have not differed materially from those of Golgi, Cattaneo and Ciaccio. Concerning the form of the end-organs, we may say that the true spindle-shape is not quite uniform, the amount of enlargement in the equatorial region varying so much that at times we find the spindles reduced to long, slender cylinders, having nearly the same dimensions throughout their length, but usually tapering slightly at the ends. This cylindrical form seems especially common in the dog. The length of the organ, according to Cattaneo, varies from $80\ \mu$ to $800\ \mu$, the width, from $50\ \mu$ to $400\ \mu$. These figures seem to us not correctly given in the text cited and do not correspond with the proportions of those end-organs figured by Cattaneo. Kölliker gives his measurements of the human spindle as 1.28 mm. to 1.42 mm. long and 0.17 mm. to 0.25 mm. wide at the mus-

cular end, while in the rabbit, the end-organs were 0.24 to 0.79 mm. long and 0.02 to 0.11 mm. broad, while Golgi gives them as varying in length from 300μ to 800μ and in breadth from 80μ to 120μ . Ciaccio mentions a neuro-tendinous organ found in a woman, which was 2 to 3 mm. long and 1-10 to 1-5 mm. wide. As our own observations have to do largely with the termination of the nerve in the neuro-tendinous end-organ, we have made no measurements of the end-organs studied by us, but have added here some measurements given by other observers; this to call attention to the great size of this end-organ, especially in man. In preparations stained in methylen-blue and fixed in ammonium picrate, cleared and teased and mounted in glycerine ammonium picrate, the end-organs are usually, as we have stated, somewhat flattened; we have therefore felt that our measurements would not be wholly accurate; in longitudinal sections it is somewhat difficult to obtain a section of the entire end-organ in one preparation.

Compound spindles, as mentioned by Ciaccio, have been not infrequently noticed by us, and we have represented (Plate XVII, Fig. 23) a triple one taken from the rat.

We have found neuro-tendinous end-organs in the tendons of practically all muscles studied, but they are especially numerous, or at least more easily found, in connection with certain muscles, as for instance in the large fascia of the back muscles and in the tendons of the interossei of the foot of the rabbit and in the tendons of the gastrocnemius, tibialis posticus and extensor longus digitorum of the cat. Something of the number and relative position of these organs may be seen from a figure given by Golgi and reproduced by Barker in his Text-book of the Nervous System, of the back muscles of the rabbit. Preparations similar to that reproduced by Golgi, we have often made.

The position of the neuro-tendinous end-organ is, in nearly all cases, in the transition zone between muscle and tendon, and one extremity is attached to muscle, while the other becomes continuous with tendon fasciculi. But Ciaccio notes that in the tendon of the superior rectus (eye) in man, he has found certain

end-organs which are tendinous at both extremities and we have observed the same fact in a few cases.

In all the mammalia we have studied, we have found no neuro-tendinous end-organs which were not encapsulated. Ciaccio, however, mentions the peculiar fact that in the bat, he finds the spindles in the anterior extremity non-encapsulated, while those in the posterior extremity always possess a distinct investing sheath. While we have observed no such marked variation in the end-organs of the mammalia which we have studied, we do find a marked difference in the thickness and density of the capsule, it being at times so thin that our most careful manipulations failed to preserve it intact; at others, so dense that it held the intrafusal tendon bundles in place in spite of much more violent treatment. Cross sections also show a marked difference in the thickness of the capsule, at times showing only one or two layers of connective tissue fibers with a few nuclei, at others, several layers arranged rather densely around the spindle and surrounded by still other layers of looser connective tissue. This variation was noticed, not only in different muscles of the same animal, as observed by Ciaccio, but even in different parts of the same muscle.

The capsule consists of from one to several layers of white fibrous connective tissue, in which we have been unable to demonstrate any yellow elastic fibers, either by Unna's orcein stain for elastic tissue or by the methylen-blue, which often stains yellow elastic fibers a pale blue. Between the bundles of white fibrous connective tissue in the capsule, are connective tissue cells. Both Golgi and Cattaneo have demonstrated, by means of silver nitrate, that this capsule is enveloped by a layer of large polygonal endothelial cells.

In the axial space, we find a varying number of tendon fasciculi, the intrafusal tendons, which differ from ordinary tendon in having a greater number of nuclei, the fasciculi being smaller, both nuclei and fasciculi staining more readily and more intensely so that they are readily differentiated from the surrounding tendon. We now and then find in certain regions of the intrafusal tendon fasciculi what Kölliker has described as a

“mehr zusammenhängende Masse von Schnensubstanz.” In such regions, the tendon looks even more like embryonic connective tissue than in places where the fasciculi are smaller, stain more deeply and possess more nuclei. Cattaneo has noted that the neuro-tendinous end-organs vary in size and in the complexity of the nerve ending with the different species of animals studied, being larger in the rabbit than in the guinea pig and larger than either in the dog, whose spindles approach in size and complexity those found in man. That they also vary with the age of the animal, Cattaneo mentions, being smaller and less complex, the younger the animal. This fact we have observed, especially with regard to the cat, having investigated the end-organs in numerous young kittens, in which they were uniformly much shorter, the capsule thinner and the nerve ending simpler than in the adult cat.

Concerning the blood supply of these organs, we have nothing to add to the observations of Cattaneo.

Nerve Structure.—As Golgi stated, the nerve destined to supply these organs can be readily distinguished from ordinary motor nerves as it passes through the muscle, the fiber being large, rarely branching and the internodal segments shorter than those of the motor nerve, as it approaches its termination.

Although in general, we agree with the writers quoted that the neuro-tendinous end-organ is usually supplied by one nerve, which divides at a variable distance from the organ, yet we hardly think it so unusual for two or more independent nerves to innervate one spindle as we are led to believe from the emphasis placed upon this fact by Cattaneo and others. The nerve fibers, as said before, may divide first after entering the spindle, or may divide at variable distances from the organ, into two or more medullated fibers, which, as they enter the spindle, lose their sheath of Henle, which becomes continuous with the capsule of the spindle, but retain their medullary sheath for a time. The nerve usually enters the end-organ near its center, more rarely toward its muscular extremity.

The nerves which innervate the neuro-tendinous end-organ usually approach it from the muscular side, often turning

sharply at right angles to their course and entering the spindle from a direction at right angles to its long axis. At other times, the branches turn back to spindles behind their point of branching, forming a long curve not unlike what Cattaneo likens to the branches of the weeping willow. At other times, the nerve approaches the spindle from the same direction as its long axis, when it either enters at the extremity or passes along beside the organ to near the center and then turns sharply and enters the end-organ. In nearly all cases in which the nerve enters the the end-organ near its center, it at once divides into two primary medullated branches, which turn toward the the two extremities of the organ. These fibers may extend with shorter and shorter internodal segments and with few side branches to near the extremities of the organ, before breaking up into a number of finer branches, each of which redivides, the resultant tertiary branches soon becoming non-medullated and terminating as we shall describe later. The few side branches given off nearer the center are either non-medullated or quickly become so and soon terminate in the typical end-arborization. This massing of the end-brushes at the two extremities of the spindle, the center being comparatively free, gives a peculiar appearance, although it is not at all uncommon, especially in the cat. Such a spindle is represented in Plate XVI, Fig. 21. At other times, and this may perhaps be considered a more typical form of the ending, the nerve fiber divides at once on entering the end-organ, the branches turning toward the extremities of the spindle, but the primary medullated branches are very short and soon divide into a number of secondary branches, some passing back toward the center and some on toward the extremities and all quickly dividing into a number of non-medullated fibers which soon form the characteristic plaque. In this form, the equatorial region of the organ is occupied by a dense and confused mass of terminal ramifications, mingled with the large but short medullated fibers, the whole mass gradually diminishing in size as it approaches the poles. In other end-organs, the nerve branches before entering the organ, or two or more independent nerves enter the organ so that three or four large medullated

fibers enter near the center, divide into secondary and tertiary branches, which soon become non-medullated and terminate, the whole ending resembling a bush or low tree whose trunk is at right angles to the long axis of the organ. In still other organs, less frequently found, the nerve enters near the extremity and either branches at once or runs for some distance before branching, sending off at intervals side branches with their terminal plaques and finally breaking up into a large number of non-medullated fibers and ending in the typical end-arborization. This gives a more distinctly tree-like appearance than any of the other forms seen. These are the four principal types of end-organs seen by us in the mammalia studied and they may, any or all of them and many modifications of them, be seen in any of the species examined. They may even all be seen at times in different parts of the same tendon, so that none of them can be said to be distinctive of any species of mammalia nor of any special part of the same animal, the form of the ending depending largely on the accidental arrangement of the medullated nerves and their relation to the ending.

In addition to the nerves found ramifying in the end-organ, nerves may sometimes be seen running through the sheath or capsule of the organ and sometimes fine varicose fibers crossing the organ, whose ending we have not observed, but which seem to be quite independent of the nerve supplying the end-organ, and which may be a part of the "*réseau nerveux*" described by Ruffini as occurring occasionally about the neuro-tendinous end-organs of the cat, and terminating on the striated muscle either near the organ or at some distance from it. If so, its occurrence does not seem to be confined to the end-organs of the cat. In the dog, a peculiar long cylindrical form of end-organ seems to predominate, in which the large medullated nerves enter the organ more or less obliquely, divide into two or three medullated branches, which pass nearly unbranched in various directions through much of the length of the organ, giving off at intervals side branches which are either non-medullated or quickly become so and there is very little branching of

either medullated or non-medullated nerves, so that the typical arborization effect is nearly lost. We have observed this type of end-organ in none of the other animals studied.

While the general structure of the neuro-tendinous end-organs and the general arrangement of nerves in the organ are the same for all mammalia studied by us, the terminal nerve apparatus differs somewhat in the different animals and is quite characteristic for each species. We will therefore describe the nerve end-plaque for the different forms somewhat in detail.

In the dog, as stated above, long medullated nerves pass through the organ almost unbranched, lose their sheath of myelin, but as still rather large and nearly unbranched axis cylinders pass toward the extremity of the organ and either end unbranched in a terminal granular enlargement, round or pear-shaped, or irregular expansions of the axis cylinders, or branch into a number of varicose fibers, fine axis cylinders, on which are seen numerous round, oval, pear-shaped, irregularly polygonal or leaf-like enlargements, which may rest directly on the fine nerve fiber or may be raised from it by a very fine nerve filament in which case it resembles still more a leaf or flower attached to a stem by a long, slender pedicle. At the extremity of each non-medullated branch, as at the end of the main nerve fiber, the axis cylinder widens out into the peculiar granular enlargement characteristic of this ending in all its forms. This terminal enlargement may be a simple round or oval ball or the whole fiber may broaden out for a considerable length, having thorn- or leaf- or plate-like masses attached to it, at the sides, at the ends, in an irregular confused way, wherever room can be found for one to lodge. The whole non-medullated nerve may twine about and between the fasciculi in a serpentine manner, penetrating the fasciculi, while the characteristic enlargements clasp the bundles of tendon fibers composing the fasciculi. In addition to the terminal arborization, all along the long, large non-medullated fiber, short fine side branches are given off, which end as do the parent fibers. Besides these, many processes are given off from the main stem, of different shapes, all granular, some with slender, short pedicles, support-

ing the most varied form of enlargement, some broad and ungainly, resting directly on the nerve trunk, sometimes simply rectangular processes, but oftener other bits or masses of granular matter, sharp and pointed or oval or irregular, are attached to it in all conceivable ways and places, making an indescribably irregular ending. Some of these side processes twine themselves about or enclasp the fasciculus, while others are simply spread out upon it, the whole ending resembling somewhat a long, climbing vine, with broad, strong tendrils, enclaspings the fasciculus against which the vine rests, and bearing leaves and flowers of the most fantastic patterns to adorn its surface. We have represented in Plate XVI, Fig. 20, a typical end-organ taken from a dog, which had been injected with methylen-blue, the tissues fixed in ammonium molybdate, dehydrated, and cleared and teased in xylol and mounted in balsam. In this method, there is no softening of tissues and all the parts bear their normal relation to each other.

In the neuro-tendinous end-organ of the cat, the main stem of the nerve usually forms a much less prominent part of the picture, the finer medullated branches, with their still finer non-medullated divisions and the terminations with their graceful curves and fanciful twining tend to cover and conceal the straight rude, ungraceful outline of the large trunk, which in the end-organ just described, formed such a prominent part of the ending. In Plate XVI, Fig. 21, is shown, however, an end-organ from the cat, in which the large medullated nerve, nearly unbranched, occupied the greater part of the equatorial region of the organ. Usually the large nerve branches and rebranches, bush-like, the branches becoming finer and finer, finally losing their sheath of myelin, and as axis cylinders, further divide and twine in long, graceful curves, and become beset with enlargements of the most varied size and form; some in long strings, like strings of beads, the enlargements small, granular and mostly round or oval and connected by the fine axis cylinders, these simply lying on the surface of the tendon fasciculus or twining in undulating curves about it or between adjacent fasciculi and sometimes sending off larger processes which partially

encircle the tendon bundles, thus realizing to a very limited extent the truth of Ciaccio's description "*à anneaux ou à spirale.*" Sometimes the non-medullated nerves run for some distance and then widen out at the extremity into large, granular, flower-like masses. As a rule, however, in the cat the terminal processes are rather short and simple, compared with those of the rabbit and dog and the enlargements rather small, often sessile or with very short stems, and quite irregular, often leaf-like. The endings are quite distinct, being rather small and well separated, the one from the other. In the young kitten, a characteristic end-organ from which is shown in Plate XVII, Fig. 24, the entire ending is shorter and simpler. While the medullated nerve branches quite as much as in the typical end-organ of the adult, the terminal axis cylinders are short and but slightly branched, often bearing at their extremities a single oval or pear-shaped or clover-leaf granular enlargement, sometimes having a few enlargements along their length, the larger ones encircling the tendon bundles and the whole spray twining slightly about the fasciculus. The difference in complexity, then, which has been mentioned, seems to depend entirely upon the difference in the length and branching of the non-medullated fiber and the difference in number and size of the peculiar granular enlargements which characterize this ending.

In the rabbit, the form of neuro-tendinous end-organ, which we have observed most frequently, is distinctly fusiform, the nerve or nerves entering in the equatorial region and soon branching into two or three or more secondary branches, terminating by dividing into two or more non-medullated nerves, which extend unbranched for considerable distances, bearing at very short intervals enlargements of varied form and size, round, oval, club-shaped, or very irregular masses, most of them supported by a short pedicle. These are so closely packed and so regularly placed about the fiber that the whole tuft has a peculiar, long, cylindrical shape, but curves slightly in long, sinuous lines, through the organ, while the side processes partially encircle one or more of the small tendon bundles. This form of terminal plaque is repeated with some variations at

each branching of the nerve fiber. Often numerous such endings lie close together and uniformly parallel to each other, the whole resembling somewhat a poplar with its long, slender, leafy, nearly parallel branches, or rather two such trees placed base to base, with their tops extending toward the extremities of the spindle. A not infrequent form of end-organ met in the rabbit, has one or more large medullated nerves enter the organ at the muscular extremity, extend unbranched through about one-third the length of the organ and then break up suddenly into numbers of these long, slender, densely packed, non-medullated nerves. At times, mingled with the more characteristic tufts, we see a single nerve rise from the medullated trunk, pass out unbranched and terminate in a rather large, club-shaped enlargement. In other spindles, we see endings more closely resembling those in the cat, being shorter, wider and less compact and spread out more over the surface of the tendon than those we have described. The end-organ shown in Plate XVI, Fig. 22, represents a rabbit's spindle in which three medullated nerves enter the organ, each, after repeated subdivision, breaking up into the end-arborization, the final non-medullated fibers, with their lateral and terminal varicosities being shorter and simpler than those found in many of the end-organs of the rabbit. But in all the end-organs studied, whatever their form, we find the characteristic plate-like enlargements, besetting the varicose fibers, larger and more complex and more closely packed together than those in the cat, resembling more in complexity and in the long, slender cylindrical plaques, the end-organ of the dog.

In the rat, the terminal tuft is comparatively simple. In the triple end-organ, represented in Plate XVII, Fig. 23, we have three large medullated nerves entering the organ, each dividing into two or three secondary branches, one of which passes to one division of the organ and one to another, so that there is a somewhat intricate intercrossing of nerves. The termination of each nerve is, however, comparatively simple, having few side branches. The non-medullated fibers twine slightly about and between the fasciculi and are beset with broad, irreg-

ular, leaf-like enlargements, which encircle the bundles of connective tissue making up the tendon fasciculi of the end-organ. The terminal enlargements remind us slightly of those found in the simpler ending of the turtle, a characteristic form consisting of a broadening and flattening out of the whole axis cylinder, which becomes granular and is fantastically adorned on all sides by other granular masses of different shapes and sizes.

In addition to these endings, we see an occasional varicose fibril, winding through the connective tissue and showing none of the terminal enlargements. This simple, varicose fibril, which seems not connected with the proper ending of the end-organ, we have observed occasionally in end-organs from other species of mammalia studied, and it seems to us to have no important relation to the end-organ or the nerve ending therein, but to be perhaps analogous to the fine nerve fibers which Ruffini has described in the end-organs of the cat as forming a "*réticule nerveux*" and ending on the striated muscle. It has occurred to us, however, that they may be vaso-motor fibers of the arterioles of the end-organs, only partly stained.

Longitudinal sections of the neuro-tendinous end-organs of mammalia, as sketched in Plate XVIII, Figs. 27 and 28, show that the varicose fibrils, while slightly undulating, often lie upon the tendon fasciculus, and may seem to pass between two adjacent bundles, but never seem to form a complete spiral. The terminal plates are seen to pass between the tendon bundles. The character of the ending appears the same as in surface preparations.

In cross sections, as illustrated in Plate XVII, Figs. 25 and 26, we see a thin connective tissue capsule, enclosing a variable number of tendon fasciculi, which stain readily and show nuclei more frequently than the adjacent tendon. In other cross sections of the series, the fasciculi seem broken up into smaller tendon bundles, which may or may not be surrounded by loose connective tissue. As Ciaccio has said, and as our sections show, the nerve branches run in the connective tissue binding the small bundles of tendon fibers together, finally penetrating the fasciculus and partially surrounding the smaller bundles. The ring de-

scribed by Ciaccio seems to us rather like a clamp, partially surrounding the tendon, while the spiral is neither uniform nor well marked. The nerve plaque seems in each case to surround fasciculi near the superficial surface of the end-organ, and never or seldom those in the interior, while the larger medullated fibers are found mostly in the deeper parts and their secondary and tertiary branches approach the surface, finally ending in the plaques above described on the smaller tendon bundles of the fasciculi nearest the surface of the end-organ.

In all these neuro-tendinous end-organs, with all their variations in size and complexity, the same characteristics are noted: Medullated fibers, branching and rebranching, becoming non-medullated, the non-medullated fibers being beset by larger or smaller granular enlargements of varied form; these granular masses were interpreted as nuclei by the older writers, but we believe with Ciaccio that they are accumulations of neuroplasm. The complexity of the organ depends largely on the number of medullated branches, while the complexity of the nerve plaque depends rather on the length and number of the non-medullated fibers and the number and size of the characteristic granular enlargements besetting them. In the amphibia only, have we observed no characteristic granular enlargements on the varicose fibrils constituting the plaque. In amphibia, the ultimate branches of the nerves ending in the neuro-tendinous end-organs are not unlike the ultimate branches of the nerves ending in the neuro-muscular end-organs of these vertebrates as described by Smirnow and the writers, which also differ markedly from the nerve terminations in the neuro-muscular end-organs of other vertebrates.

The nerve endings in the tendons of the eye-muscles, concerning which Ciaccio speaks especially, saying that in man they are found either in the neuro-tendinous end-organs of Golgi, or free on the primary tendon bundles, while in other mammalia, they are only 'in the neuro-tendinous end-organs, have been fully described for the cat by one of us in another communication.

Relation to other sensory endings.—Golgi and Cattaneo both mentioned the intimate relation existing sometimes between the neuro-tendinous end-organs and certain small sensory endings resembling small rudimentary Pacinian corpuscles and usually spoken of as Golgi-Mazzoni organs. Ciaccio also refers briefly to this fact and Ruffini has dwelt upon it with considerable emphasis in each of the series of three papers before alluded to. In our preparations, we have observed neuro-tendinous end-organs in close proximity to large Pacinian corpuscles, to small Pacinian or Golgi-Mazzoni organs, to Krause's cylindrical and spherical end-bulbs, and to neuro-muscular spindles. Some of these preparations deserve a little fuller mention. In one preparation, two medullated nerves separated themselves from the main trunk and ran together for a considerable distance. One of these finally left the other and divided into two branches, one of which bore at its extremity a large spherical end-bulb of Krause. The other branch divided, each subdivision innervating a cylindrical end-bulb of Krause, in close proximity to a large neuro-tendinous end-organ, which was supplied by the nerve which had accompanied that supplying the three Krause end-bulbs. In the same preparation and almost in the same field of the microscope was a neuro-muscular spindle, having an independent nerve supply.

We have often seen neuro-tendinous end-organs and neuro-muscular spindles in close proximity, sometimes lying side by side, oftener end to end, and often enclosed in the same connective tissue capsule. In most cases noted, however, the two end-organs have had an independent nerve supply no matter how closely related they might seem to be; or if the nerve supply has not been independent, it has been difficult to demonstrate the contrary fact. In one particularly fortunate preparation, however, we were able to see a neuro-muscular spindle and a neuro-tendinous end-organ, lying end to end, in the same capsule, where it seemed to us that one medullated nerve fiber ran along beside them sending off fibers at right angles to itself to innervate the neuro-muscular spindle and then at the other extremity of the capsule, a nerve was given off which supplied

the neuro-tendinous end-organ and ended therein in the characteristic arborization and end-plaques.

We have, also, observed in a few cases, the fact mentioned by Cattaneo and emphasized by Ruffini, that the so-called Golgi-Mazzoni organs are found sometimes in and sometimes under the capsule of the neuro-tendinous end-organs. Our observations, however, even with the most perfectly stained preparations, have not led us to conclude that this relation is so constant, even in the end-organs of the cat, as Ruffini's descriptions would seem to indicate. We have found many end-organs perfectly stained, in which no trace of a Pacinian or Golgi-Mazzoni organ was to be seen. In other preparations, these organs were found in or under the capsules. The fact that this is a region where sensory nerves and sensory endings seem to abound; that sensory endings of many kinds are found here, sometimes in relation with the neuro-tendinous end-organs and sometimes not; and that the nerve supply, as Cattaneo has stated, is usually independent, would lead us to conclude, as did Cattaneo for the neuro-muscular spindle, that the relation is purely accidental.

As to the encapsulation of the neuro-tendinous end-organs, different opinions are expressed by the different authors who have worked on this subject. Golgi and later Cattaneo, finding that the nerve endings in tendon, in the lower types of vertebrates (amphibia and reptilia) were free, while those in the higher types (birds and mammalia) possessed a distinct capsule, drew the natural conclusion that the capsule was the result of a higher development of the organ; that the end-organ in mammalia was but the result of a condensation of connective tissue about the tendon fasciculi and a number of the free endings thereon, in the amphibia. Ciaccio, however, having observed the fact, already cited, that in the bat, the end-organs of the anterior extremity were free, while those of the posterior extremity were encapsulated, decides that Golgi and Cattaneo were wrong and that the capsule is not the result of such development and condensation.

As noted before, we have found the tendon nerve endings

free in the frog, generally free but occasionally encapsulated in the turtle, generally encapsulated but occasionally free in the bird and always encapsulated in the mammal; that in the young kitten, the capsule is thinner and more imperfect than in the adult cat and that end-organs taken from different parts of the same body may differ in the thickness of the capsule; and that, whether free or encapsulated, the nerve invariably ends on tendon fasciculi having the same characteristics and differing in the same way from ordinary tendon. There seems to be here a gradual transition corresponding to the development of the animal. We think it true also in general that those end-organs which have the most perfect capsule are the most complex and well developed as regards their nervous structure. Since end-organs of different degrees of complexity of nerve endings are often found in the same animal as well as of different degrees of perfection of the capsular envelope, we can not agree with Ciaccio that his finding is a logical argument against the idea that the encapsulated neuro-tendinous end-organs of the higher types of vertebrates are developed from the free endings in the lower forms and that the capsule is one indication of that development.

Function.—All those who have investigated the neuro-tendinous end-organs seem agreed that they are sensory in their nature. The resemblance of general structure to that of other known sensory organs, the fact that the nerve supplying this organ resembles in character those supplying other sensory organs and can often be traced from the same nerve bundle, and still more conclusive, the fact that we have observed the same nerve fiber supplying this organ which supplies a neuro-muscular spindle, proved sensory by Sherrington's physiological experiments, all seem to make the conclusion fairly certain, while, if any doubt remained, the experiments of Cattaneo, showing the degeneration of the nerves and endings in the end-organs, after section of the peripheral nerve trunk, while they remained unaltered after section of the anterior roots, should set them at rest.

As to the special function of the neuro-tendinous end-organs, there are many differences of opinion. Sachs believed that they regulated the distension of tendons in the contraction of the corresponding muscles. Golgi regarded them as instruments of special nerve reverberation of tendon to muscle and was supported by Erb, Westphal, Schultze and Fürbringer. Cattaneo regarded them as organs of muscle sense, while Ciaccio believed that they proportioned the amount of distension and resistance of the tendon to the amount of contraction of the corresponding muscle. We will not venture to add one more to this list of conflicting opinions, none of which are supported by proofs, but will merely say that Ciaccio's opinion seems to us reasonable. As to the manner of producing this effect, their general structure, the peculiar clamp-like endings surrounding the peripheral bundles of the organ seem to render it probable that they, like the neuro-muscular spindles, are peculiarly adapted to respond to impulses mechanical in their nature.

Conclusion and Summary.

From the results of our investigations on the four classes of vertebrates studied, we think we are warranted in the following conclusions :

I. In the four classes of vertebrates studied, the tendons are supplied with a special nerve end-organ consisting of several tendon fasciculi, embryonic in nature, which in birds and mammalia are generally surrounded by a connective tissue capsule, while they are usually not so surrounded in reptilia and never in amphibia.

II. These end-organs have an independent blood supply as shown by Cattaneo and an independent nerve supply.

III. They are usually innervated by a single nerve fiber, which may branch before reaching the organ or after penetrating the capsule. There may, however, be two or more independent nerves.

IV. These nerves, after repeated branching, end in a manner which, in its minuter details, differs for the different

types observed, but in general consists of one or many tufts of non-medullated fibers which, in all the forms studied, except the frog, are beset with large, irregular, sessile or pedunculated granular end-disks, not resembling the varicosities on ordinary non-medullated fibers, but still consisting of accumulations of neuroplasm. These terminations are either applied to the surface of the tendon fasciculus or enclasp it or a part of it in a clamp-like manner and end on the smaller bundles of fibrillar connective tissue composing the tendon fasciculi. In the frog, the ending consists of groups of tufts of simple varicose fibers.

V. The neuro-tendinous end-organ is sensory in function, but its special function is not yet decided.

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DESCRIPTION OF FIGURES.

All figures were sketched, at the level of the table, with the aid of the camera lucida and are from preparations stained in methylen-blue. All figures giving surface views of neuro-tendinous end-organs, unless otherwise stated, were drawn from preparations fixed in a saturated solution of ammonium picrate, cleared, teased and mounted in ammonium-picrate-glycerine.

REFERENCE LETTERS.

- c.*—capsule of neuro-tendinous end-organs.
m.—striated muscle fibers.
mn.—medullated nerve fibers.
nR.—nodes of Ranvier.
t.—tendon.

PLATE XIII. *Amphibia*.

Figs. 1 and 2.—Terminations of nerve fibers in neuro-tendinous end-organs of frog, from *tibialis posticus*. Only the nerve fiber and its terminal branches reproduced. Leitz No. 7 objective; No. 2 eye-piece. Figure 1, reduced to $\frac{1}{4}$ original size; figure 2, $\frac{1}{3}$ original size.

Fig. 3.—A portion of longitudinal section of neuro-tendinous end-organ of frog, stained in methylen blue, fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Leitz 1-12 oil immersion; No. 2 eye-piece. Reduced to $\frac{3}{4}$.

Fig. 4.—Cross section of neuro-tendinous end-organ of frog. Prepared as in Fig. 3. Leitz 1-12 oil immersion; No. 2 eye-piece. Reduced to $\frac{3}{4}$.

PLATE XIV. *Reptilia* (*Emys meleagris*).

Fig. 5.—Nerve fiber with terminal branch and irregular end-disks from tendon taken from posterior extremity of turtle. Preparation was compressed before sketching to bring out more clearly the general distribution of the nerve branches and their terminations. Leitz No. 7 objective; No. 2 eye-piece. Reduced in figure to $\frac{1}{3}$ the size of drawing.

Fig. 6.—Nerve termination from neuro-tendinous end-organ of turtle, from preparation fixed in ammonium molybdate, teased and mounted in balsam. Leitz No. 7 objective; No. 2 eye-piece; reduced in figure to $\frac{1}{3}$ the size of drawing.

Fig. 7.—Longitudinal section of neuro-tendinous end-organ in fascia-like tendon. Shows relative position of nerve ending in tendon. Tissue fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{2}{5}$ of the size of drawing.

Fig. 8. Preparation made as in Fig. 7. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{1}{2}$ the size of the drawing.

Figs. 9, 10 and 11.—Cross sections of neuro-tendinous end-organs of turtle. Tissue fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Fig. 11 shows an imperfectly encapsulated neuro-tendinous end-organ. Leitz 1-12 oil immersion; No. 2 eye-piece. All reduced to $\frac{3}{4}$ of size of drawing.

PLATE XV. *Bird (Dove).*

Figures in Plate XV are from neuro-tendinous end-organs obtained from the tendons of the wings of doves.

Fig. 12.—Small neuro-tendinous end-organ, with no, or imperfectly developed capsule, compressed under cover-glass to bring out more clearly the general arrangement of nerve branches and terminations. Leitz No. 7 objective; No. 2 eye-piece. Figure $\frac{1}{2}$ the size of drawing.

Figs. 13, 14 and 15.—Neuro-tendinous end-organs of dove, showing difference in size and shape and complexity of nerve terminations. Leitz No. 7 objective; No. 2 eye-piece. Figure 13 reduced to $\frac{1}{3}$, Figs. 14 and 15 to $\frac{1}{2}$ the size of drawings.

Figs. 16 and 17.—Longitudinal sections of neuro-tendinous end-organs of dove; from sections made by fixing tissue in ammonium molybdate, sectioning and staining in alum carmine. Show relation of end-organs to the tendon and muscular fibers. Leitz No. 7 objective; No. 2 eye piece. Figures reduced to $\frac{1}{3}$ the size of drawings.

Figs. 18 and 19.—Cross sections of neuro-tendinous end-organs of doves. Sections prepared as for figures 16 and 17. Leitz 1-12 oil immersion; No. 2 eye-piece. Figures $\frac{1}{2}$ the size of drawings.

PLATE XVI. *Mammalia.*

Fig. 20.—Neuro-tendinous end-organs from interossei muscles of posterior extremity of a dog. From preparation fixed in ammonium molybdate, teased and mounted in balsam. In this figure, the shape and general structure of this end-organ, as found in the dog, are well reproduced. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{1}{3}$ the size of drawing.

Fig. 21.—Neuro tendinous end-organ of cat. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{1}{3}$ the size of drawing.

Fig. 22.—Neuro-tendinous end-organ of rabbit. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{1}{3}$ size of drawing.

PLATE XVII. *Mammalia.*

Fig. 23.—Compound neuro-tendinous end-organ from fascia of back muscles of white rat. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{1}{3}$ of size of drawing.

Fig. 24.—Longitudinal section, cut parallel to the surface of the tendon of one of the leg (posterior extremity) muscles of kitten about one month old. Attention is called to the simple terminations as compared with other figures given. Tissue was fixed in ammonium molybdate sectioned and counterstained in alum carmine. Leitz 1-12 oil imm.; No. 2 eye-piece. Figure $\frac{1}{3}$ size of drawing.

Figs. 25 and 26.—Cross sections of neuro-tendinous end-organs of rabbit from tissue fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Leitz 1-12 oil imm.; No. 2 eye-piece. Figures reduced to $\frac{1}{2}$ size of drawings.

PLATE XVIII. *Mammalia.*

Fig. 27.—Longitudinal section of neuro tendinous end-organ of cat, from tissue fixed in ammonium molybdate, sectioned and mounted in balsam. Section not counterstained. For this reason, the nuclei are not shown in the figure. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{1}{2}$ the size of drawing.

Fig. 28.—Longitudinal section of neuro-tendinous end-organ of rabbit. Specimen prepared as in figure 27. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to $\frac{1}{2}$ size of drawing.

A NEW BRAIN MICROTOME.

By HENRY H. GODDARD, A.M., Ph.D.,

Formerly Fellow in Clark University.

With Plates XIX and XX.

There are now in use several forms of microtome for sectioning a brain or other large organ. Some of these are merely enlarged copies of the instruments in use for ordinary histological work. Others are modified to some extent in order to better adapt them to the more difficult work of producing so large a section in perfect form. This difficulty is by no means small, and in most of the instruments now to be had, is only partially overcome.

It is generally considered necessary to have the section cut into liquid—water or alcohol—so that it can be floated out smoothly. Two well known machines embody this principle. One is the von Gudden. In this instrument the object to be cut is embedded in a well of sufficient size to contain it, the top of which is crowned with a rim of plate glass. By means of a micrometer screw the object is raised in the well while the glass rim serves as a guide for the knife which is moved “free hand” over its surface. Outside of the glass rim is a good sized pan which is filled with alcohol or water to such a depth as to cover the knife. The section is thus cut under water and floats off without injury.

A more recent instrument is one invented by Bruce.¹ It differs from the Von Gudden, chiefly in replacing the “free hand” cutting by a machine cut. It consists of a heavy metal tank 2 cm. deep, 20 cm. wide, 90 cm. long. A square middle section is 6 cm. deeper than other portions of the tank. This

¹ Described and illustrated in *Journal of Nervous and Mental Disease*, Vol. 25, No. 12, Dec., 1898.

contains the object holder. The knife has a width of 5 cm. and a cutting edge of 30 cm. It requires from 1.5 to 2 litres of fluid to fill the tank. In cutting, the knife is drawn back by a treadle and when released "the weight and pulley gives the cutting stroke," In the description referred to, the writer says "Exceedingly thin sections may be cut on it without skipping." But he does not tell us just how thin. He further adds that the object-holder is not sufficiently delicate in its adjustment, for the finest embryological work.

The machine we are about to describe was made two years ago at Clark University, in response to the demand for a microtome that would cut a whole human brain, in any plane, into sections of, say, 50 micra thickness, without wasting a section from beginning to end, and with the consequent possibility of determining the location of every section.

This instrument embodies two principles new to brain microtomes. First the brain is made to move instead of the knife. Secondly, the knife is made to hold the fluid into which the section is to be cut. The advantages of this arrangement are easily seen. The blade being fixed at both ends can be made sufficiently long and thick to insure a clean oblique cut, without sagging or springing out of correct position. Being placed horizontal it can be flowed with alcohol, a small quantity being sufficient to float the section.

The details of construction and the *modus operandi* will be readily understood from the following description and from reference to the cuts.

The finished microtome is 34 inches high and 35 inches long, and is made wholly of iron. The cutting blade is made of finely tempered steel, 36 inches long, $2\frac{1}{2}$ in. wide and $\frac{7}{8}$ in. thick at the back. It is strongly concaved on the upper surface, and slightly so on the under surface. To the back edge is screwed a zinc pan flush with the concaved upper surface of the blade. This with the concavity of the blade itself, forms the receptacle for the alcohol into which the section slides as it is cut. This pool is 8 inches wide, and $\frac{1}{4}$ inch deep at the back, and in front shoals gradually to the very edge of the blade.

This gives sufficient room to manipulate the largest section of a human brain, and a very small quantity of alcohol—a pint at most—is sufficient for all requirements.

The carriage for the brain, comprises two parts: an *inner* part to which the brain is fastened, and which slides up and down within an *outer* part. The outer part slides horizontally along a track from one end of the machine to the other. The inner part is box-like, $7 \times 6 \times 6\frac{1}{2}$ inches, open on two sides. It is very accurately adjusted to the outer case, within which it is moved up and down by a micrometer screw. The head of the screw is graduated so that a single click gives a section of 12.5 micra. The outer case is $11.5 \times 7.5 \times 7$ inches. It slides between the two rails which form the track, and it extends about half its length below them, thus securing great stability and smoothness of movement. It is moved along the track by means of a rack and pinion similar to that used on lathes.

The dimensions of this carriage and the excursion of the inner part are such that the largest human brain may be mounted in any position, and sectioned completely from one end to the other without waste or loss of material. Small sections are cut equally well.

In constructing the machine, the blade was first put in position since it must be exactly level in order to hold the alcohol. The "cut" must be oblique, therefore the blade was placed obliquely from the back left hand corner to the front right hand corner of the supporting frame. In order to give the brain a movement parallel to this *obliquely placed* cutting edge, the track slopes downward from left to right; and in order for the brain to pass under the knife and clear the bevel, the track slopes downward from front to back. The amount of these two inclinations can be judged from the pictures.

In operating the machine, the brain is first embedded in celloidin and mounted as nearly as possible in the plane in which it is desired to section it, on a slab of suitable material—vulcanized wood fiber is used at present, but this is liable to warp if specimen is kept long in 80% alcohol. This slab is then fastened to the top of the inner part of the carriage by

means of clamps or screws. This plan enables one to use specimens at will, not being compelled to finish with one before another can be cut, as is generally the case with those machines which embed the object in a well.

Small adjustments for changing the plane of section, may be made by moving the blade, one end of which is slotted so as to be clamped in different positions. One end of the blade being fixed, sliding the other end *forward* or pushing it *backward* has the effect of changing the plane of section. This is convenient also for adjusting whenever the brain has been removed from the machine and it is desired to replace it so as to continue cutting in the same plane as on a former occasion. Larger adjustments are conveniently made by wedging the fiber as it is clamped to the carriage.

The sections thus made are easily handled by floating a sheet of paper under them, by which they may be lifted from the alcohol, stained and mounted in balsam like any other specimen. For gross anatomy an unstained section mounted in gum glycerine makes a very nice preparation showing white and grey matter in their natural colors.

The slides thus made furnish a clean, neat and easily handled specimen which can serve to demonstrate either macroscopic or microscopic structures. A series, taken at intervals of, say from one to two centimeters, and in each of the three directions, gives about as complete a picture of the anatomy of the brain, as could be desired.

The cost of this first machine has been about \$150. Considerable difficulty was experienced in finding anyone who would undertake to make a blade of such large dimensions, warranted to be of uniform temper throughout, and to preserve a perfectly true and straight edge, without warping or twisting out of shape. After consulting several of the manufacturers of microtome knives, both abroad and in this country, we finally found in Worcester a firm that was willing to undertake the work. Accordingly the blade was made by Loring Coes & Co. It consists of a soft iron body (thus doing away with the danger

of warping) into which is welded an edge of finest razor steel. It is without flaw and is a model of accurate workmanship.

After two years use, this microtome continues to be satisfactory. Were we to make another machine now, only two variations from the foregoing description would be made. It would in no way be a detriment to have the blade thicker on the back—one inch or even an inch and an eighth. It would probably be an advantage in the matter of keeping it sharp—the edge not being quite so thin would not nick as easily. Secondly, the supporting frame might be somewhat heavier. There is a slight vibration, which, while of no inconvenience as yet, may in time have some effect upon the delicacy of the adjustments.

The writer is very largely indebted to Dr. C. F. Hodge, at whose suggestion the work was undertaken, for constant help and suggestion in designing the machine, as well as valuable aid in bringing out the completed microtome.

West Chester, Pa., December Fourth, 1899.

EXPLANATION OF PLATES.

PLATE XIX. Figs. 1 and 2.

Two views of the machine with brain in place ready for sectioning.

A.—Blade, with pan attached, filled with alcohol.

B.—Brain in position for cutting.

C.—Wood fiber upon which brain is mounted.

D.—Inner "box" which is raised and lowered by micrometer screw *I*.

E.—Outer case which slides on the track *F*. (Fig. 2.)

F.—Track. (Fig. 2.)

G.—Rack and pinion for moving carriage along *F*.

H.—Graduated head of micrometer screw.

I.—Micrometer screw. (Fig. 1.)

K.—Clicking attachment. (Fig. 2.)

PLATE XX.

Fig. 3. Shows a sagittal section of the brain about $100\ \mu$ thick cut on this microtome, and reproduced in the following manner: The unstained section mounted in gum glycerine was printed directly onto velox paper, the paper being put into the plate holder and exposed through the camera like a plate. The mounted section was set up in front of the camera with the blue sky for background. Finer details of course do not come out in the reproduction, although they are beautifully shown in the section. The photograph is reduced to about $\frac{3}{4}$ natural size.

A PROPOSED NEUROLOGICAL BIBLIOGRAPHY OF THE ICHTHYOPSIDA.

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The object of this work may be briefly stated to be:

(1) To draw up a list, and if possible a complete list, of all the papers ever published which relate, either directly or indirectly, to the brain, cranial and spino-occipital nerves, spinal cord and spinal nerves, the sympathetic, and lateral sense organs of fishes and amphibia. All papers, whether morphological, anatomical, physiological and embryological, and whether they directly fall within the scope of the bibliography, or only have an incidental connection with it, and whether further they are complete or only preliminary, will be recorded in such a way as to make, it is hoped, confusion on the part of a librarian or author a matter of some difficulty. The brain will include the hypophysis but not the epiphysis, and the nose, eye, and ear, will also be omitted.

(2) To intimate in each case the type or types described and figured by the author, to reduce such names to their correct synonymy, and to index the whole at the end with cross-references to the old terms.

(3) To give full information as to preliminary notices, abstracts, unaltered reprints, translations, etc., so as to obviate the necessity of a worker looking up the same paper in sometimes as many as six forms.

(4) To give at least some idea of the contents and scope of each paper, and references to all principal criticisms passed upon it.

(5) For the convenience of British students to indicate where the rarer works and journals may be found in the London libraries.

As, of course, the lateral line system may be traced in many fossil fishes, the literature of which I was largely unacquainted with, I sought the co-operation of Dr. Ramsay Traquair, F. R. S., to whose accurate and laborious researches fossil ichthyology owes so much, and who kindly referred me to all the relevant publications, and drew up a list of all the types in which the system had been described and figured.

Besides the difficulty of the fossil literature, another stumbling block, which must inevitably in some instances, but I hope not in many, prove fatal, is that it frequently happens that an author's text not only goes beyond his title (which presumably often cannot be helped), but that the title itself may be absolutely misleading. For example, who would suppose that a work entitled, "De musculis et glandulis observationum specimen" contained a description of the cranial nerves of the skate? It is obviously impossible to make the bibliography complete in this respect, where contemporary authors with unequivocal titles have not referred to them in their texts or lists of literature. Again, Prof. Max Fürbringer has recently published a work entitled, "Ueber die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie." The original observations in that magnificent work extend considerably beyond: (1) the spino-occipital nerves, and (2) the Selachia and Holocephala. The result of such action as these two authors have exemplified is that the bibliographer has practically to read through every work he consults, and to consult twice as many works as he records.

With regard to the question of dates, it often happens that as many as three or even four dates may be given to one paper. For instance, there may be the official year of a Society (which often indicates the volume instead of consecutive numbers), the date of the part in which the paper appears, the date on which the paper itself is published, and the date at the foot of the title page of the volume. I have disregarded any difference in date which does not run into a different year, but have otherwise given all possible dates which may be quoted for a paper. For example, if a paper is quoted as 1884 (Hft.)

1885 (Bd.), it means that the *Heft* containing it was published in 1884, whilst the *Band* containing it is dated 1885. Two such dates seem to be quoted indifferently by authors referring to such a work.

Again, it often happens in the case of German separate works and dissertations of about 30 to 50 years back, that they were published several times at different towns within a period of a few years, although each edition was in every respect essentially the same, except for the imprint on the title page. In these cases each edition is recorded, and indicated by the place of publication and the date.

Of course, such works as Carus and Engelmann's "*Bibliotheca Historico-Naturalis*," the Royal Society's catalogue, Agassiz's "*Bibliographia Zoologiae*," etc., are immensely useful to any zoologist, whether compiling a bibliography or not. The principles upon which the latter work was written often astonish me. It is a strange mixture of completeness, important omissions and mistakes. Recently in following out the numerous ramifications of Johannes Müller's "*Ganoid bible*" it referred me to a volume of the Linnaean Society's Transactions, which I presumed contained an abstract, translation, or a discussion of that famous work. On looking it up, it was found to refer to nothing more than a mere list of books, amongst which the work in question figured, recently added to the library of the Society!

The difficulty of running down a species in the case of the older authors is often somewhat tedious, and that it is really always necessary to do so is evident when we remember that the descriptions of the older authors are often both detailed and valuable. Thus, A. von Haller, writing in 1768, gives a description of the brain of a fish which he says is the species of *Trocta* called Ombre (misprinted Omble) Chevalier in the Lake of Geneva. Quite a small investigation is necessary before it can be determined to what fish he is referring. Attention has been specially directed towards this alphabetical list of types and synonyms, since it is hoped that this will prove of some value to neurologists working at lower vertebrates.

Several works will be included which are not concerned directly with the Ichthyopsida, but with the results of which it is important that a worker in the group should be acquainted.

At present, as the result of three year's vacation work, some 800 works have been seen and recorded, and about 200 of these have been worked through and indexed. It seems very likely that the complete bibliography will contain 1600 references, so that its completion without more leisure will take some time. It is hoped to include works up to the end of the century (by which I mean to the end of the current year).

The length of the list in a bibliography so circumscribed is such that it seems imperative to halt before pursuing any further the paths of research, and to consider what has already been effected. It is safe to say that much of the work now being done has been done before and often done well, and if the bibliography, even only in some measure, helps us to realize where we are, it will have been well worth doing. Let us, therefore, keep in mind the fate of the men who started out to build a tower to heaven, and finished by perpetuating a babel upon earth.

THE NUMBER AND SIZE OF THE NERVE FIBERS INNERVATING THE SKIN AND MUSCLES OF THE THIGH IN THE FROG (*RANA VIRESCENS* *BRACHYCEPHALA*, COPE).

By ELIZABETH HOPKINS DUNN, M.D.,
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SUMMARY.

1. The innervation of the thigh in the American frog, *Rana virescens*, shows no marked variation from that of the European frog, *Rana esculenta*.

2. An enumeration of all the nerve fibers concerned in innervating the hind legs reveals only a slight numerical inequality for the two sides.

3. The nerve fibers concerned in the innervation of the skin and muscles of the thigh are more numerous and of greater average caliber than those innervating the remainder of the leg. Hence in the leg of the frog the fibers of greater diameter run the shorter course.

4. The nerve fibers to the muscles of the thigh surpass both in number and average diameter those which supply the skin of the thigh.

5. From the results of enumeration we conclude that of the fibers which innervate the thigh about 8% divide, one division passing in the main trunk of the sciatic nerve at least to the level S_2 (Fig. II), distal to the last branch of the sciatic nerve. Direct observation reveals some large fibers dividing dichotomously where the branches from the sciatic to the thigh are given off. They are sufficient in number to render the explanation probably correct.

6. The cutaneous nerve fibers of the thigh bear to the cutaneous area which they supply a relation of one fiber to each 1.13-1.58 square millimeter of this area.

SECTION I. GROSS ANATOMY OF THE MUSCULAR AND CUTANEOUS NERVES OF THE THIGH.

The muscles and skin of the thigh in *Rana virescens* are innervated by branches from the crural and sciatic nerves, and thus derive their fibers from the VIIth, VIIIth, and IXth spinal nerves.¹

¹ Gaupp numbers the spinal nerves from II to XI, beginning the enumeration with the Hypoglossal as the *second* spinal nerve, because of its exit between the first and second vertebrae. See Gaupp's edition, Ecker's und Wiedersheim's *Anatomie des Frosches*, Part II, p. 156.

A. A Comparison of Rana virescens with Rana esculenta and Rana temporaria.

With minor variations, to be noted later, the innervation of the skin and muscles of the thigh in *Rana virescens* corresponds to that of *Rana esculenta* and *Rana temporaria* as given in Gaupp's edition of Ecker's und Wiedersheim's *Anatomie des Frosches*,¹ 1896-99. A concise presentation of the innervation in *Rana virescens* is offered in Table I. The nomenclature adopted is that used by Gaupp in the description of *Rana esculenta*.²

TABLE I.

Branches of Crural and Sciatic Nerves.

- C. Nervus cruralis s. N. femoralis anterior.
 - a) Ramus cutaneus femoris lateralis.
 - b) R. muscularis to the M. tensor fasciae latae.
 - c) Rr. musculares to the M. iliacus internus and the M. iliacus externus.
 - d and e) Rr. musculares to the M. adductor longus and the M. pectineus.
- S. Nervus ischiadicus s. N. femoralis posterior.
 - 1. Branches to the plexus ischio-coccygeus.
 - 2. R. cutaneus femoris posterior.
 - 3. R. muscularis to the M. pyriformis.
 - 4 and 5. Rr. musculares to the M. gemellus and the M. obturator internus.
 - 6. R. profundus posterior.
 - a) R. adductorius.
 - 1)—to the M. adductor magnus.
 - 2)—to the M. quadratus femoris.
 - 3)—to the M. obturator externus.
 - b) R. descendens communis.
 - 1) R. anterior.
 - α —R. muscularis to the caput ventrale of the M. semitendinosus.
 - β —Rr. musculares to the caput ventrale of the M. abductor magnus.
 - γ —R. muscularis to the M. sartorius.
 - 2) R. posterior.
 - α —Rr. musculares to the caput dorsale of the M. semitendinosus.
 - β —Rr. musculares to the M. gracilis major.

¹ Part II, pp. 194-197.

² See Gaupp's edition, Part II, pp. 196-197.

- γ —Rr. musculares to the M. gracilis minor.
 δ —R. cutaneus femoris medialis.
 c) Rr. musculares to the M. semimembranosus.
 7. R. muscularis to the M. ileo-femoralis.
 8. R. profundus anterior.
 α —R. muscularis to the M. glutaeus magnus.
 β —R. muscularis to the M. cruralis.
 [x—R. muscularis to the M. ileo-fibularis.]

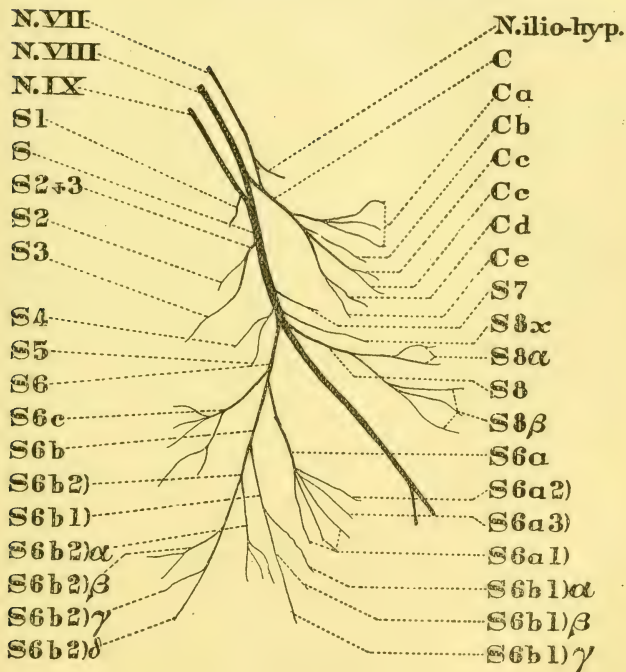


FIGURE I.

From a dissection of the right plexus lumbo-sacralis of *Rana virescens*, showing all the muscular and cutaneous branches which innervate the thigh. The designations are those used in Tables I and II. The magnification is one and one-half times the actual size of plexus.

Two of the figures¹ accompanying the text mentioned give a partly diagrammatic representation of the relations of the right crural and sciatic nerves as seen when the skin of the thigh is removed, and the more superficial muscles are severed.

In Figure I, drawn from a dissection of the right plexus lumbo-sacralis of *Rana virescens*, we here present in some detail, the ramifications of the crural and sciatic nerves, and show the relative size of the branches, their lengths and points of ramification, but not their exact anatomical relations, as the branches have been severed from their muscle terminations and extended in a single plane.

1. Variations appearing in successive dissections of *Rana virescens*.

The order of branching in the plexus lumbo-sacralis of *Rana virescens* remains nearly constant, although the points at which the branches leave the trunks are subject to some displacement. In ten dissections, no two specimens were found to be exactly alike, even when the right and left plexuses of the same individual were compared. Figure I shows the conditions which were most frequently found present.

2. Differences between *Rana virescens* and the standard furnished by *Rana esculenta*.

Using Table I, derived from Gaupp, as a standard, the innervation of *Rana virescens* differs in the following particulars:

Crural Nerve. In *Rana virescens* the trunk of the crural nerve usually divides dichotomously. One of the resulting branches, dividing into two or three coördinate branches, supplies cutaneous areas, the second subdivides to furnish muscular branches.

In other instances the cutaneous branches are given off from the trunk in two or three distinct bundles, the trunk finally cleaving to furnish branches to the muscles.

Sciatic Nerve. a. In *Rana virescens*, the branch to the plexus ischio-coccygeus (S 1) has its origin from the IXth spinal

¹ Figures 55 and 56, Gaupp's edition, Part II, pp. 194 and 195.

nerve, as is represented in Figure I. This branch is disregarded in all our computations because it is not concerned in the innervation of the muscles of the thigh.

b. The branch to the M. pyriformis (S 2) is given off with the R. cutaneus femoris posterior (S 3), and takes its departure from the latter at the point where the cutaneous branch passes under the M. pyriformis on the way to its peripheral distribution. In no instance was it found arising directly from the trunk of the sciatic nerve, as occurs in *Rana esculenta*.

c. The branch to the M. iléo-fibularis springs from the sciatic trunk proximal to the R. profundus anterior, or springs as a subordinate branch from this ramus. In no dissection was it found springing from the sciatic trunk distal to the R. profundus anterior, the condition pictured in *Rana esculenta*.¹

d. The second branch to the caput ventrale of the M. adductor magnus, given in broken lines in Figure I, and designated (S 6 b 1) β) is absent in *Rana virescens*. The anterior and terminal portion of the R. descendens communis from which this branch is given off in *Rana esculenta* passes over the M. adductor magnus in order to reach the M. sartorius, but no branch to the former muscle was found in *Rana virescens*.

e. In the ten dissections examined, the branches to the M. gemellus and the M. obturator internus were found to come from a common stem, whereas in *Rana esculenta* they more frequently arise independently.

*B. Review of the accounts of the innervation of the thigh which are given in successive editions of Ecker's Anatomy of the Frog.*²

As the successive editions of Ecker's Anatomy of the Frog show wide variations in the nomenclature and innervation of the muscles of the thigh, and the recent edition of Gaupp,

¹ See Figure 56, Gaupp's edition, p. 195.

² (a) Die Anatomie des Frosches. Dr. Alexander Ecker. Braunschweig, 1864.

(b) The Anatomy of the Frog. Dr. Alex. Ecker, translated and revised by George Haslem, M.D., Oxford, 1889.

(b) A. Ecker's und R. Wiedersheim's Anatomie des Frosches, edited by Dr. Ernst Gaupp. Braunschweig, 1896-99.

1896-99, has been referred to as a standard in this paper, a comparison of the various texts is presented in Table II. The designations for the muscles, given in the right hand column of this table, are identical with those in Table I and Figure I, and indicate the source of nerve supply for each muscle. For the sake of brevity these designations will be used in subsequent tabulations. The branch to the M. ileo-fibularis, of which no mention is made by Gaupp, is given the designation S 8 x, and so appears in Figure I and Table II.

TABLE II.

The Muscles of the Thigh and their Innervating Nerve Branches.

Names of muscles, Ecker, 1864.	Names of muscles, Gaupp's edition of Ecker, 1896-99.	Designations of nerve branches, Gaupp, Pt. II, 1897.
	LONG MUSCLES	
	<i>Lateral surface</i>	
Triceps femoris	Triceps femoris	
Vastus internus	Caput anticum seu cruralis	S 8 β
Rectus femoris anticus	Caput medium s. Tensor fasciae latae	C b
Vastus externus	Caput posticum s. Glutaeus magnus	S 8 α
	<i>Medio-ventral surface</i>	
Sartorius	Sartorius	S 6 b 1) γ
Adductor longus	Adductor longus	C d
Adductor magnus	Adductor magnus	S 6 a 1). S 6 b 1) β
Rectus internus major	Gracilis major	S 6 b 2) β
Rectus internus minor	Gracilis minor	S 6 b 2) γ
	<i>Medio-dorsal surface</i>	
Biceps	Ileo-fibularis	S 8 x (omitted from Gaupp, 1896-99.)
Semimembranosus	Semimembranosus	S 6 c
Semitendinosus	Semitendinosus	S 6 b 1) α . S 6 b 2) α
	SHORT MUSCLES	
	<i>Superficial layer</i>	
Ileo-psoas	Iliacus internus	C c
Glutaeus	Iliacus externus	C c
Quadratus femoris	Ileo-femoralis	S 7
Pyriformis	Pyriformis	S 3
	<i>Middle layer</i>	
Pectineus	Pectineus	C e
Adductor brevis {	Obturator externus	S 6 a 3)
	Quadratus femoris	S 6 a 2)
	Gemellus	S 4
	<i>Deep layer</i>	
Obturatorius	Obturator internus	S 5

1. Alterations in nomenclature.

The nomenclature of the muscles has been subject to many changes due to the increase in our knowledge of the general anatomy of the frog, and to the advances in comparative anatomy. These changes are clearly shown in Table II.

The division (in Gaupp's edition, Part II, p. 156) of the former *M. adductor brevis* into three distinct muscles is worthy of note. The anatomical lines of demarcation are not easily discernible, but the innervation from three distinct sources marks the developmental individuality of the muscles.

2. Alterations in the account of the innervation.

In the earlier editions the study of muscle innervation is not at all complete. In the earliest, the edition of 1864, the innervation of the *M. sartorius*, the *M. rectus internus major*, the *M. gluteus*, and the *M. pectineus*, is not given.

In the same edition, p. 45, the innervation of the *M. adductor brevis* is credited to the crural nerve, while the branches to the *M. obturator* and the *M. quadratus femoris* are said to rise together. Haslam, in his revision of 1889, p. 189, repeats these errors.

Ecker, 1864, in his list of nerve branches, p. 49, does not mention the first branch of the sciatic nerve, the one to the plexus ischio-coecygeus. Haslam's revision, p. 192, supplies this omission, but does not mention the branch to the *M. pyramidalis* which Ecker does mention.

Gaupp, *Abtheilung II, Nervensystem*, 1897, furnishes in his text no description of the innervation of the *M. ileo-fibularis*, corresponding to the descriptions of the branches to the other muscles. In the figure on page 195, the branch in question is represented as the most distal branch of the sciatic nerve, and in the description of the *M. ileo-fibularis*, Gaupp's edition, *Abtheilung I, Skelet und Muskelsystem*, p. 183, the innervation is credited to the sciatic nerve.

As the thigh of the frog is a most excellent place to practice accurate dissection, it has seemed worth while to give the foregoing description of the nerves and muscles in one of the

common North American frogs, so that beginning students might not be entirely dependent upon the description of the European forms which appear in the books most likely to be consulted.

SECTION II. NUMBER AND SIZE OF THE NERVE FIBERS INNERVATING THE THIGH.

A. Introduction.

The thigh region was selected as the one most available for the numerical comparison of nerve fibers because the muscle masses are of sufficient volume to make the study of their innervation simple, and the nerves, both muscular and cutaneous, can be identified with comparative ease. Possible comparison with results already obtained through investigations in this laboratory made a complete study of the distribution of all the fibers of the lumbo-sacral plexus very desirable. This involved so much labor that the attention was confined for the time being to the innervation of the thigh alone.

The entire series of observations to determine the number and size of the nerve fibers was first carried through on the nerves of the left and right thighs of one frog (Sex, female. Length, 20.5 cm. Weight, 49.7 grams) with the expectation that the results from the two sides would serve as mutual controls. The numerical results, although symmetrical for the two sides, were in some particulars so unexpected that a second series of enumerations was made to test the accuracy of the first series. In the second frog (Sex, female. Length, 20.5 cm. Weight, 45.4 grams) the innervation for both the right and the left thighs was studied. This second series of observations confirmed the numerical results of the first series. The determination of areas was not undertaken in the investigations upon the second frog.

I. Levels at which the computations were made.

The levels at which the computations to determine the number and area of the fibers were made, are indicated in Figure II, by the interruptions in the continuity of the nerve branches. The nerve designations correspond to those already used in Figure I, and Tables I and II, with the excep-

tion of S_1 and S_2 , which have been added to indicate the points of section of the sciatic nerve above and below its branches. The levels were so selected as to include all the fibers from the plexus lumbo-sacralis which innervate the skin and muscles of the hind leg of the frog.

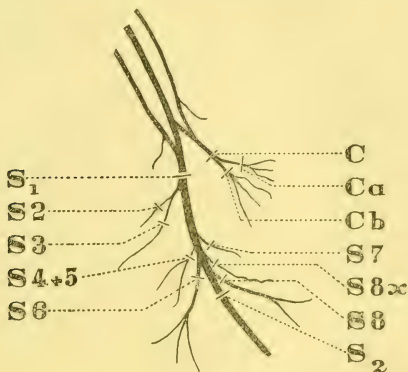


FIGURE II.

From a dissection of the right plexus lumbo-sacralis of *Rana virescens*, showing the primary branches of the Crural and Sciatic Nerves. The interruptions in the nerve branches mark the levels at which the computations for the number and the size of the fibers were made. The designations are those used in Figure I, and Tables I and II, with the exception of S_1 and S_2 , which are added to indicate the levels of section of the Sciatic Nerve above and below its thigh branches.

The crural nerve was sectioned just proximal to its division into branches, and each branch was cut as close as was practicable to its point of departure from the main trunk. Sections of the sciatic nerve were made both proximal and distal to its branches to the thigh, the latter being made for the purpose of determining the number and size of the fibers which pass to the shank and foot. The proximal sections was made distal to the first branch of the sciatic nerve, the branch to the plexus ischio-coccygeus, which does not contribute to the innervation of the thigh. Each one of the branches of the sciatic nerve, which contributes to the innervation of the thigh, was cut close to its point of separation from the sciatic trunk,

Special sections were made of all the cutaneous subdivisions of these main branches of the sciatic nerve at the levels where their character as cutaneous nerves could first be recognized.

2. Methods of observation.

The frog was chloroformed and its length and weight ascertained. The ovarian tissue was removed and weighed, and its weight deducted from the total weight. The length was measured from the tip of the nose to the end of the longest digit. After division and retraction of the skin, the superficial muscles were separated sufficiently to bring the nerve trunks into view but not so widely as to put on tension the nerve branches supplying the muscles. Upon the nerve tissue thus exposed a solution of osmic acid, 1%, was dropped. A certain portion of the solution was retained in the cavity formed by the retracted tissues, and fresh solution was added from time to time until fifteen or twenty minutes of exposure to the action of the reagent assured the fixation of the tissue in its normal condition. The portions selected, indicated in Figure II, were now carefully removed, and, after being placed in 1% osmic acid, were left in a dark chamber for twenty-four hours. At the expiration of that time the material was washed in distilled water for two hours. After dehydrating in increasing percentages of alcohol and clearing in xylol, the material was embedded in paraffin by the usual process, care being exercised to identify in every instance the proximal and distal ends of each portion.

The sections were cut with the Minot microtome to a thickness of $3\frac{1}{3}$ micra, fastened to the slide with albumen fixative, cleared in xylol and mounted in colophonium.

a. Enumeration. Two methods were used for enumerating the nerve fibers.

The "net method" was employed for all sections of an area small enough to present the entire surface in the field under a magnification of 460 diameters.

The photographic method was found to be more satisfactory for all larger sections. This method has already been de-

scribed by Dr. Hardesty¹ as used in his enumeration of the fibers forming the spinal nerves.

In using both methods, special attention was given to the recognition of the smallest medullated fibers, which so readily escape observation under ordinary circumstances.

b. Determination of areas. For the determination of the areas of the sections whose fibers had been counted, drawings at a magnification of 165 diameters were first made by the aid of a camera lucida. The boundary line was located at the periphery of the most external fibers and within the epineurium. By this method the area measured was limited to that actually occupied by the fibers, plus the space between the fibers. The area covered by this camera drawing was determined by the planimeter. This form of integrator for measuring the area of a plane surface by carrying a pointer around its boundary and reading the indications from a scale, furnishes a most convenient instrument for determining the areas of nerve sections.

On the basis of the magnification the true area of the section was estimated. The estimate was controlled by the measurements of diameters made directly on the section itself.

B. Number of Nerve Fibers.

The study of the number of nerve fibers supplying the thigh in *Rana virescens* is based upon data obtained by an examination of two frogs, frog B, Sex, female. Length 20.5 cm. Weight, 49.7 grams, and frog C, Sex, female. Length, 20.5 cm. Weight, 45.4 grams. A count was made at corresponding levels for the two sides and the numbers given in the tables are the result of actual enumeration. The tables dealing with numbers alone are those from III to VII inclusive. The levels at which sections and counts were made are illustrated and explained by Figure II and the text accompanying that figure.

I. Comparison of the number of nerve fibers for the right and the left sides.

The total number of nerve fibers innervating each leg is nearly the same. In the case of frog B, the number for the left

¹ The Number and Arrangement of the Fibers forming the Spinal Nerves of the Frog (*Rana virescens*). IRVING HARDESTY. *The Journal of Comparative Neurology*, Vol. IX, No. 2, 1899.

leg is 5385, for the right leg 5273. (See Table III). For frog C (Table III), the number for the left leg is 5987, and for the right leg 6011. By reference to Table IV, similar variations are found in the thigh branches for the corresponding sides. For frog B, the thigh branches of the sciatic nerve supply 1609 fibers to the left side and 1643 fibers to the right side. For the same frog the crural fibers for the left side number 991, for the right side 980. For the left side in frog C, the sciatic thigh fibers are 1600, for the right side 1576, while in the same frog 1177 crural fibers innervate the left thigh, 1238 crural fibers, the right thigh.

In the individual branches the same symmetry for the two sides prevails. In two instances, see Table IV, frog B, S 8 x, and frog C, S 8, in both of which only muscular fibers pass, the count on the two sides tallies exactly. In the larger sections the greatest difference is not more than 5% (frog C, crural nerve). While, for the sections containing less than 100 fibers, in which the percentage variation would be very great, the greatest difference was found in frog B, S 7, left side 47 fibers, right side 54 fibers.

No significance can be attached to any seeming excess in the number of fibers supplying either the right or the left side, as in successive observations the excess is not constant for either side. The simplest explanation for these differences between the two sides is that of individual variation.

TABLE III.

Showing the number of fibers in the Crural Nerve, and in the Sciatic Nerve above and below its branches to the thigh, and the calculated number of fibers to the thigh.

Designations corresponding to Fig. II.	Designation of Frog.	B		C	
		L	R	L	R
S ₁ C	Side examined				
	Sciatic fibers above thigh branches	4394	4293	4810	4773
	Crural fibers to the thigh	991	980	1177	1238
S ₂	Total to thigh, shank, and foot	5385	5273	5987	6011
	Sciatic fibers to shank and foot	2974	2868	3401	3368
	Calculated no. fibers to the thigh	2411	2405	2586	2643

2. Relation of the number of fibers innervating the thigh to the number which innervates the remainder of the leg.

The first determination of the number of fibers innervating the thigh was made in the following manner: To the number of fibers in a section of the sciatic nerve, S_1 , just proximal to the branches for the thigh was added the number of fibers in a section of the crural nerve. As all the fibers of the crural nerve are concerned in the innervation of the thigh, this section was made at a level just above that at which branching occurred. From this number, which is the sum of all the fibers innervating the entire leg, was subtracted the number of fibers which innervate the shank and foot. The latter number was ascertained by a count of a section at S_2 , a level of the sciatic nerve distal to the thigh branches. The result of this computation, shown in Table III, gives the calculated number of fibers to the thigh.

In frog B the left sciatic and crural nerves together contain 5385 nerve fibers. After the branches to the thigh are given off (S_2) there are found 2974 fibers which pass on to supply the shank and foot. The right sciatic and crural nerves of the same frog contain 5273 fibers, 2868 of which pass on to the shank and foot. The process of subtraction would show that for the left side 2411 fibers, for the right side 2405 fibers had gone to innervate the tissues of the thigh, or that in the innervation of the thigh fewer fibers were concerned than in innervating the remainder of the leg. The computations for frog C show a similar relation.

TABLE IV.

Showing the number of fibers in the crural and sciatic branches to the thigh and the total number of thigh fibers.

Designation of Frog.	B		C	
Side examined	L	R	L	R
S 2 and 3	292	306	400	389
S 4 and 5	181	189	132	124
S 6	717	740	711	709
S 7	49	54	51	50
S 8	298	282	241	241
S 8 x	72	72	65	63
Total of sciatic branches	1609	1643	1600	1576
Crural fibers	991	980	1177	1238
Total number of fibers to the thigh	2600	2623	2777	2814

For a second determination of the number of thigh fibers, counts were made of the fibers in all the crural and sciatic branches which innervate the tissues of the thigh. The numbers obtained by this enumeration are given in Table IV. In the comparison of the number of thigh fibers for frog B, 2600 fibers for the left side, 2623 fibers for the right side, with the number for the shank and foot, left side 2974 fibers, right side 2868 fibers, is found the verification of the statement that the thigh fibers are fewer in number than those innervating the remainder of the leg.

When the calculated number of fibers to the thigh—left side 2411 fibers, right side 2405 fibers—is compared with the number ascertained by direct count—left side 2600 fibers, right side 2623 fibers—the number determined by count is found in each case to surpass by about two hundred fibers the estimated number. This surprising disparity in the case of frog B led to a repetition of the enumeration of the fibers for a second frog C, lest some mistake in counting or some flaw in technique might have resulted in an error. For the second frog also, the number by count was found to exceed by about two hundred fibers that determined by estimation. The actual number for frog C is shown in Table IV to be 2777 fibers for the left thigh, 2814 fibers for the right thigh, while the calculated number, Table III, is only 2586 fibers for the left side, 2643 fibers for the right side.

3. Significance of the disparity between the computed and the actual number of fibers.

This disparity, consisting in an excess of actual, over computed fibers, is shown in Table V.

TABLE V.

Comparison of the calculated and the actual number of fibers to the thigh with the numerical excess of the latter.

Designation of Frog.	B		C	
	L	R	L	R
Side examined				
Actual number of fibers to the thigh—from Table IV	2600	2623	2777	2814
Calculated number of fibers to the thigh—from Table III	2411	2405	2586	2643
Number of fibers in excess of calculated fibers	189	218	191	171

The amount of this excess is not great, varying in the different observations from a minimum of 171 fibers to a maximum of 218 fibers. This would include from 6% to 8% of the number of fibers actually concerned in the innervation of the thigh. But the fact that such an overplus was found in each thigh for each frog calls for some explanation. In the absence of any error this excess can only be accounted for by a branching of nerve fibers and indicates that in each sciatic nerve approximately two hundred fibers have branched. An attempt was made to hit upon some method which would demonstrate the presence of such branching. The process of teasing, which seemed most feasible, was tried and abandoned as unsatisfactory, because of the mass of nerve fibers in the sciatic trunk. The separation of the fibers into small bundles and the spreading of each bundle in turn under cover-glasses gave better results, but this method was open to the objection that any dividing fibers whose branches ran in different bundles would be destroyed by the separation. However a number of fibers of large caliber were discovered by this method dividing dichotomously near the point of separation of some one of the sciatic branches. These branching fibers were sufficient in number to render probable the explanation just given.

4. Proportion of the number of cutaneous to the number of muscular fibers.

The facts ascertained by making a distinction between the muscular and the cutaneous fibers are embodied in Tables VI and VII.

TABLE VI.

Tabulation of muscular and cutaneous nerve fibers to the thigh for Frog B.

Sciatic branches.	No. of muscles innervated.	Muscular fibers.		Cutaneous fibers.	
		L	R	L	R
S 2 and 3	1	123	118	169	188
S 4 and 5	2	181	189		
S 6	8	634	640	83	100
S 7	1	49	54		
S 8	2	298	282		
S 8 x	1	72	72		
Total	15	1357	1355	252	288
Crural fibers	5	372	392	619	588
Total to thigh	20	1729	1747	871	876

TABLE VII.

Tabulation of muscular and cutaneous nerve fibers to the thigh for Frog C.

Sciatic branches.	No. of muscles innervated.	Muscular fibers.		Cutaneous fibers.	
		L	R	L	R
S 2 and 3	1	86	97	314	292
S 4 and 5	2	132	124		
S 6	3	615	608	96	101
S 7	1	51	50		
S 8	2	241	241		
S 8 x	1	65	63		
Total	15	1190	1183	410	393
Crural fibers	5	368	352	809	886
Total to thigh	20	1558	1535	1219	1279

In frog B, Table VI, the left side exhibits 1729 muscular fibers, 871 cutaneous fibers, the right side 1747 muscular fibers and 876 cutaneous fibers. In the case of frog C, Table VII, 1558 muscular, 1219 cutaneous fibers innervate the left thigh, and 1535 muscular, 1279 cutaneous fibers, the right thigh. The fibers innervating the muscles are shown by both tabulations to exceed in number those innervating the skin.

5. Relation of the number of cutaneous fibers to the cutaneous area innervated.

For the determination of the cutaneous area of the thigh a frog of approximately the same length as that of frog B and frog C was selected, Sex, female. Length 18 cm. Weight 39 grams. The measurements were made upon the left leg. The lines marking the location of the hip and knee joints were selected as the upper and lower limits of the thigh area. The rounding dorsal and ventral surfaces of the thigh were reduced to flat surfaces by compression between two glass plates. The exterior of the upper plate was coated with a thin layer of paraffin. In this paraffin was traced the outline of the flattened thigh. This outline was then transferred to paper, and the area embraced within it determined by means of the planimeter. This area multiplied by two gave the area for the dorsal and ventral surfaces of the thigh. While the plates were still in place the distances between them at the anterior and posterior limits of the thigh were measured at each lateral surface by an

accurate millimeter scale. The vertical of the two measurements for each lateral surface was then computed. The length of each of these surfaces was the same as the corresponding lateral line of the outline of the thigh. Having thus ascertained the lengths and the mean width, the areas of the lateral surfaces were easily computed. In the total area given in Table VIII the decimal parts of a millimeter are disregarded.

TABLE VIII.

Relation of cutaneous fibers to the areas supplied.

Rana vis. D	Cutaneous area in sq. mm.	Number of fibers.		Sq. mm. to each fiber.	
		frog B	frog C	frog B	frog C
Left leg Thigh	1374	871	1219	1.58	1.13

The total cutaneous surface of the left thigh in frog D was found to be 1374 square millimeters. If this area was innervated by the 871 cutaneous thigh fibers of frog B, the average area to each fiber would be 1.58 square millimeters. If supplied by the 1219 cutaneous thigh fibers of frog C, the cutaneous surface to each fiber would be 1.13 square millimeters, or in short the cutaneous surface receiving its innervation from each fiber would be from 1.1 to 1.5 sq. mm., if the fibers were evenly distributed to the surface.

C. *Size of the Fibers.*

As the determination of the size of the nerve fibers is for the purpose of comparison, the area *for* each fiber, obtained by dividing the area of the section by the number of nerve fibers at that level, is substituted for the area actually occupied by each fiber.

The computation of the area for each section was accomplished with great care. Whenever the fibers showed lines of separation, the area of each division was computed separately rather than to include an unoccupied area which would increase the average area for each fiber. Whatever spreading was unavoidable in handling such extremely thin sections was uniform

for all the sections and did not influence the comparative value of the average areas.

The areas were computed at all the levels where sections had been made on both the left and right sides of frog B.

TABLE IX.

Showing for the muscular and cutaneous branches of the Crural Nerve, the area, the number of fibers, and the average area for each nerve fiber.

Rana virescens B.	Number of fibers		Area in sq. mm.		Area for each fiber in sq. μ .	
	L	R	L	R	L	R
N. cruralis						
Cutaneous branches	619	591	.085	.085	137.	144.
Muscular branches	372	389	.066	.065	177.	167.
Total	991	980	.151	.150	152.	153.

TABLE X.

Showing for the thigh branches of the Sciatic Nerve, the area, the number of fibers, and the average area for each nerve fiber. S 2 and 3, and S 6 contain cutaneous fibers.

Rana virescens B.	Number of fibers		Area in sq. mm.		Area for each fiber in sq. μ .	
	L	R	L	R	L	R
Sciatic branches						
S 2 and 3	292	306	.031	.034	107.	113.
S 4 and 5	181	189	.025	.025	136.	134.
S 6	717	740	.150	.144	209.	194.
S 7	49	54	.012	.012	247.	216.
S 8	298	282	.061	.060	205.	211.
S 8 x	72	72	.012	.012	172.	171.
Total	1609	1643	.291	.287	181.	174.

TABLE XI.

Showing for all branches to the thigh, the actual area, the number of fibers and the average area for each nerve fiber.

Rana virescens B.	Number of fibers		Area in sq. mm.		Average area for each fiber in sq. μ .	
	L	R	L	R	L	R
Sciatic branches	1609	1643	.291	.287	181.	174.
Crural branches	991	980	.151	.150	152.	153.
Totals to the thigh	2600	2623	.442	.437	170.	166.

TABLE XII.

Showing for the Crural Nerve, and the Sciatic Nerve above and below its branches to the thigh, the area, the number of fibers and the average area for each nerve fiber.

<i>Rana virescens</i> B.	Number of fibers		Area in sq. mm.		Average area for each fiber in sq. μ .	
	L	R	L	R	L	R
Proximal section of sciatic N.	4394	4293	.676	.645	154.	150.
Section of crural N.	991	980	.151	.150	152.	153.
Total	5385	5273	.827	.795	153.	151.
Distal section of sciatic N.	2974	2868	.371	.362	125.	126.

1. Average area for each fiber innervating the thigh.

The nerve fibers to the thigh naturally fall into two divisions, those which arrive by way of the crural nerve and those which traverse the sciatic pathway, and these in turn re-group themselves, according to their destinations, into muscular and cutaneous fibers.

Directing attention to the determination of areas in the crural nerve, we find that the branches easily adapt themselves to the muscular and cutaneous classification, as they contain either purely muscular or purely cutaneous fibers. Using this arrangement for our tabulation we find, Table IX, that frog B has 619 fibers in its cutaneous branches to the thigh of the left leg. The area of these branches is .085 of a square millimeter. By process of division the area for each fiber is found to be 137 square micra. The muscular branches for the same region contain 372 fibers and have an area of .066 of a square millimeter. By a like process of division the average area for each muscular fiber is found to be 177 square micra.

The total number of fibers for the left thigh is 991 and the area .151 of a square millimeter, giving an average area of 152 square micra for each nerve fiber of the left crural nerve in frog B. The numbers for the right crural nerve of the same frog are very similar and give an average area of 153 square micra for each nerve fiber.

The cutaneous thigh branches of the sciatic nerve run for some distance with certain of the muscular branches. On this account the muscular and cutaneous classification of branches cannot be adhered to, and the sciatic branches can best be tabulated in the order of their separation. Fixing the attention as before upon the left leg we find, Table X, that the total number of sciatic fibers to the left thigh in frog B is 1609. The total area for the various branches is .291 of a square millimeter. The resulting area for each fiber is 181 square micra.

For the right thigh of the same frog the sciatic branches number 1643 fibers, cover an area of .287 of a square millimeter, and furnish an average area of 174 square micra for each fiber.

Of the thigh branches of the sciatic nerve, S 2 and 3, and S 6 contain both cutaneous and muscular fibers. The remaining branches contain no cutaneous fibers.

Table XI, combining the computations for the sciatic and the crural branches, indicates that for frog B the left thigh branches contain 2600 muscular and cutaneous fibers. As these branches have a total area of .442 of a square millimeter, we determine the average area for each fiber to be 170 square micra. The measurements for the right thigh are very similar and yield an average area of 166 square micra for each nerve fiber.

In addition to these measurements of the thigh fibers, sections of the crural nerve, and of the sciatic nerve both above and below its branches were studied. The proximal section of the sciatic nerve shows, Table XII, 4394 sciatic fibers contributing to the innervation of the left leg. This section has an area of .676 of a square millimeter. From these figures we derive an average area of 154 square micra for each sciatic nerve fiber of the left leg. The proximal section for the right leg differs but slightly, giving an average area of 150 square micra for each sciatic nerve fiber.

As no fibers from the crural nerve supply the shank and the computations for the crural leg fibers will be

those given in Table XI, and discussed in connection with the thigh averages. By reference to that table we find an average area for each crural fiber of 152 square micra for the left leg, and 153 square micra for the right leg.

The total number of fibers for the left leg is 5385. The total area for the designated sections of the crural and sciatic nerves is .827 of a square millimeter. From these figures an average area of 153 square micra may be estimated for each fiber innervating the left leg of frog B. Similar computations for the right leg give an average of 151 square micra for each nerve fiber. Therefore the average area for each nerve fiber of the leg varies only a few square micra from that of each fiber of the crural or the sciatic nerve at a level just proximal to the point of departure of the first thigh branches.

TABLE XIII.

Showing for the cutaneous branches to the thigh, the area, the number of fibers, and the average area for each fiber.

<i>Rana virescens</i> B.	Number of fibers		Area in sq. mm.		Average area for each fiber in sq. μ .	
	L	R	L	R	L	R
R. cut. fem. lateralis (Ca)	619	591	.085	.085	137.	144.
R. cut. fem. posterior (S2)	169	188	.020	.021	114.	110.
R. cut. fem. medialis (S6 cut.)	83	100	.010	.011	117.	111.
Total to thigh	871	879	.115	.117	132.	133.

TABLE XIV.

Showing for the muscular branches to the thigh, the area, the numbers of fibers, and the average area for each fiber.

<i>Rana virescens</i> B.	Number of fibers		Area in sq. mm.		Average area for each fiber in sq. μ .	
	L	R	L	R	L	R
All branches to thigh	2600	2623	.442	.437	170.	166.
Cutaneous branches	871	879	.115	.117	132.	133.
Muscular branches to thigh	1729	1744	.327	.320	189.	184.

2. Comparison of the areas for the cutaneous and for the muscular fibers to the thigh.

A second interesting relation is brought to view by a comparison of the areas for the cutaneous and for the muscular fibers to the thigh.

In Table XIII, the measurements for all the cutaneous fibers to the thigh are summarized. Both the crural and the sciatic nerves convey cutaneous fibers to the thigh. The ramus cutaneus femoris lateralis is the first branch of the crural nerve, and contains all the crural cutaneous thigh fibers. This branch innervates the ventral aspect of the thigh.

The ramus cutaneus femoris posterioris and the ramus cutaneus femoris medialis are the ramifications of the sciatic nerve which carry cutaneous fibers to the thigh. The ramus cutaneus femoris posterioris is given off with the sciatic muscular branch to the *M. pyriformis*, and innervates the dorsal aspect of the thigh. The ramus cutaneus femoris medialis is the terminal twig of the posterior division of the ramus profundus posterior and innervates a portion of the median aspect of the thigh. The point of section of the latter is not indicated in Figure II, but can be identified in Figure I by the designation S 6 b 2) δ . The section was accomplished at the point at which the twig, after piercing the *M. gracilis minor*, passes through the subcutaneous tissue, and just before it separates into its cutaneous ramifications.

The crural cutaneous fibers to the thigh have been studied in connection with Table IX, where the average area for each fiber of the crural nerve was computed. An average area was there determined of 137 square micra for each crural cutaneous fiber to the left thigh, and 144 square micra for each crural cutaneous fiber to the right thigh.

The first of the sciatic cutaneous branches to the thigh, ramus cutaneus femoris posterioris, contains for the left thigh 169 fibers in an area of .02 of a square millimeter, and furnishes an average area of 114 square micra for each fiber. The same branch for the right leg furnishes an average area of 110 square micra for each fiber.

The second sciatic cutaneous branch, ramus cutaneus medialis, has, for the left leg, 83 fibers in an area of .01 of a square millimeter, and supplies an average area of 117 square micra for each of its fibers. The average area for each fiber of the same branch of the right thigh is 111 square micra.

The totals for all the cutaneous fibers to the thigh, Table XIII, show for the left thigh a total number of 871 fibers, a total area of .115 of a square millimeter and an average area of 132 square micra for each fiber. For the right side of the same frog, the totals are approximately the same, giving an average area of 133 square micra for each fiber.

To compute the average area for the muscular fibers to the thigh, the totals for the cutaneous thigh fibers were subtracted, Table XIV, from the totals for all the branches to the thigh, given in Table XI. The differences give the totals for the muscular fibers. By this method we find that for the left thigh, the muscular fibers number 1729, and have a section area of .327 of a square millimeter. The average area for each of these fibers is 189 square micra. The muscular branches for the right thigh vary but slightly from those of the left thigh, and give an average area of 184 square micra for each fiber.

Hence we observe that the average area for each cutaneous fiber to the thigh is somewhat less than the average area for all the thigh fibers, and that a marked superiority in size is exhibited by the muscular fibers when their average area is compared with the average area for the cutaneous fibers.

3. Average area for each fiber innervating the shank and foot.

The measurements to determine the average area for each fiber innervating the shank and foot were made upon a section of the sciatic nerve at the level S_2 , Figure II, just distal to the last of the sciatic thigh branches, since all the fibers to the shank and foot run in the sciatic nerve. At that level in the left sciatic nerve of frog B, we find, Table XII, 2974 fibers in a section having an area of .371 of a square millimeter. By process of division an average area of 125 square micra is determined for each nerve fiber. The right sciatic nerve at the

same level contains 2868 nerve fibers in an area of .362 of a square millimeter, and gives an average of 126 square micra for each nerve fiber.

Hence the average area for each fiber innervating the shank and foot in frog B, is 125 square micra for the left side, 126 square micra for the right side.

4. Comparison of the average area for the fibers to the thigh with that for the fibers to the shank and foot.

The average area for each nerve fiber to the thigh has already been considered. The averages, as given in Table XI, are 170 square micra for each fiber of the left thigh, 166 square micra for each fiber of the right thigh. In contrast to this average, we find, from Table XII, that the average area for each fiber to the shank and foot is 125 square micra for the left leg, 126 square micra for the right leg. The shank and foot fibers are thus shown to be of a less caliber than those to the thigh. The significance of this superiority in size of the thigh fibers is very great when we consider that in accordance with the generally accepted law of Schwalbe,¹ the greater caliber should belong to the fibers of the nerve which has the greater extent, and so to the fibers which innervate the shank and foot. In order to complete the proof that the largest sciatic fibers innervate the tissues of the thigh, measurements for the areas were made upon the ten largest fibers in the section of the sciatic nerve above the branches. The average area for these ten fibers was 287 square micra. Similar measurements on the sciatic nerve section below the branches yielded an average area of 186 square micra, thus showing that the very largest fibers were absent at the lower level. Measurements of the largest fibers in the branches to the thigh yielded fiber areas equal to those in the section above the branches. From this observation we may justly conclude that the largest sciatic fibers do not run the longest course. The discussion of this superiority in size of the thigh fibers will be postponed until a study of the sciatic fibers to the shank has been completed.

¹ Ueber die Kaliberverhältnisse der Nervenfasern. von G. Schwalbe. Leipzig, 1882.

CRITICAL DIGEST.

A DIGEST AND A CRITICISM OF THE DATA UPON WHICH IS BASED THE THEORY OF THE AMOEBOID MOVEMENTS OF THE NEURONE.

By H. HEATH BAWDEN.

I. HISTORICAL.

The first researches which are significant in relation to the theory of amoeboid movements of the neurone are those of His (45) which show the migration of the neuroblasts from their primitive place of origin among the cells of the myelo-spongium to the point of exit of the fibers of the anterior roots.¹ Here we seem to have an instance of true amoeboid movement in the developing nerve cell.

The next literature on the subject is an article by Rabl-Rückhard (85) in the *Neurologische Centralblatt* for 1890 which relates to conditions found in the case of the mature neurone. Without ostensibly departing from the generally accepted Gerlach conception, he simply suggested the possibility of amoeboid changes in the network formed by the protoplasmic processes of the neurones, coincident with different functional states of the nervous tissue. In contrast with the current view, which looked upon the elements of the nervous tissue as fixed in form, this hypothesis possesses considerable significance. Rabl-Rückhard suggested the possible rupture of the filaments of the nervous meshwork and their welding together again, employing the very expression "amoeboid movement" to describe this process in the protoplasmic branches of the neurones. His suggestion was, however, in every sense an hypothesis, since there were at that time no researches directly supporting such a view.

About the same time there appeared an article by Wiedersheim (109) in the *Anatomische Anzeiger* for 1890, on the brain of the tiny transparent crustacean, *Leptodora hyalina*, with plates which showed clearly certain changes of or within the nerve cells in that region of the "brain" where it connects with the optic ganglion. These researches

¹Also from the spinal ganglia cells migrate to form the sympathetic system.

were utilized later by Duval in support of the theory of amoeboid movements. Observations of a similar nature had been made by two other investigators, Svierczewski and Freud, but for some reason are not referred to by Duval, though they are as conclusive as are those of Wiedersheim. Svierczewski (105) in 1869 had made observations on the cells of the frog's sympathetic ganglia kept alive in aqueous humor or lymph, in which active changes were discovered within the nucleus. The paper by Freud (37), which appeared in 1882, was on the living ganglion cells of *Astacus*. He described little rods and angular shaped shreds within the nucleus which in some instances changed their form and position with astonishing rapidity.

A paper by Tanzi (106) in the *Revista Sperimentale* for 1893 touches on the subject and is quoted subsequently by Duval. Tanzi calls attention to the growth changes which take place in the nerve cells, particularly to the approximation of the cell branches. He suggested that in the case of acts which by reason of habit or education take place more or less easily and automatically the nervous current occasioned a special nutritive activity, thus bringing about a hyper-nutrition of the cells traversed by the nervous impulse. If, now, he says, this increase in the volume of the nerve elements results, among other things, in the elongation of the protoplasmic filaments, then the continued or repeated passage of the nerve impulses within the limits of normal functioning will gradually diminish the distance between the tips of the contiguous branches of adjacent neurones. The actual functioning of the nerve pathways, thus, would tend to increase the conductivity of the chains of neurones for the nervous impulse.

A little later, in 1894, Lepine (58) of Lyon, in connection with certain observations on hysteria, set forth still other considerations as to the possibility of variations in the relations of the neurones. He suggested that a "psychical influence" might suffice to occasion that slight displacement of the terminal ramifications necessary to obstruct the passage of the nervous impulse, and that the reestablishment of this connection takes place through a certain erethism of the cell resulting in the approximation of the cell branches. It is not unreasonable to suppose, he says, that sleep is occasioned by such relative isolation of the neurones, and he thinks that the changes subsequent to this erethism would explain the extraordinary suddenness with which we sometimes pass from the sleeping to the waking state.

The next year (February, 1895) appeared the first paper of Duval (31) with the sub-title "*Théorie histologique du sommeil*." Duval's conception was apparently suggested by the fact, demonstrated by

Golgi's and Ramon y Cajal's beautiful preparations, that the neurones of the cortex do not form a continuous pathway for the nervous impulse, but that these are related only by the simple contiguity of their terminal arborizations. The central mechanism for the simplest reflex can thus no longer, he says, be conceived of as a single cell, but is rather a relation of contact ("l'articulation à distance") between these terminal arborizations. Those chemical substances, then, such as strychnine and potassium bromide which modify the reflexes operate, not on the cell body, so much as on these prolongations of the cell. This is the case also with curare, which has been shown to have its effect exclusively in the terminal arborizations of the motor nerve.¹ Now if this conception is extended to all the nervous centres we are in a better position, says Duval, to understand the anatomical or histological conditions of all such phenomena as memory, association, imagination, and even habit and education. In a similar way the accelerative effects of tea and coffee are explained. He refers to the papers of Tanzi and Wiedersheim in support of his theory and cites also the fact of changes in the cilia of the olfactory cells. The phenomena of sleep are explained in the same way. When one falls asleep the terminal prolongations of the neurones are supposed to retract. Feeble stimulation of the sleeping man calls forth certain reflexes perhaps, but is not sufficient to establish a full connection of the lower centres with the cortex. Stronger stimulation, however, has the effect of securing the elongation again of these contracted branches of the neurones. In consequence, the connection with the cortex is re-established and the person awakes. The successive stages of awakening mark the gradual reestablishments of these cortical connections after this period of interruption of greater or less duration which we call sleep. In support of the theory on the pathological side, reference is made to the researches of Azoulay (6) on general paralysis, studied by the Golgi-Cajal method, in which a part of the dendritic ramifications of the pyramidal cells had disappeared—that is, the pseudopodia of certain neurones had become atrophied. He cites also the researches of Balbiani and of Morat (71).

Langley's investigations (55) on the action of various poisons on the nerve cells and nerve endings in the frog's heart deserve attention in this connection. He shows that nicotine paralyzes the nerve cells, and not the nerve endings in the heart, while muscarin will stop the heart after the application of the nicotin, and that atropin "will put an

¹Cf. the researches which follow, by Langley.

end to the muscarin stand-still." That is, the latter poisons, muscarin and atropin, act on the dendritic branches of the nerve cells rather than on the cell bodies themselves, thus, as the author says, "giving firmer ground for the view that muscarin and atropin exert their effect on the heart, so far as the effect is nervous, by acting on the nerve endings in the muscles" (p. 279-280).

A. von Kölliker (52) in March, 1895, publishes a critique of the hypothesis of Rabl-Rückhard and Duval, in which he contends that such amoeboid movements of the nerve cell have never been observed, and that such a theory is incompatible with the doctrine of the fibrillar structure of the nerve elements.

About the same time Ramon y Cajal (18 and 19) published papers locating the amoeboid movements in the neuroglia cells, thus admitting the possibility of variations in the structure of the cortex, but not granting amoeboid properties to the nerve cells as such.

A paper appeared also during this year (1895) by Renaut (91) on the articulation of the neurones.

During 1895-1896 we have two papers by Demoor (26 and 27). He had previously touched on the subject in a paper (24) in 1893, and in a preliminary report (25) in 1895. In the research reported in the first paper mentioned (26), dogs were first subjected to the influence of morphine, chloral and chloroform. The histological changes observed in the nerve cells were the disappearance of the gemmules and the moniliform appearance of the dendrites. In a subsequent paper (27) Demoor applies these observations to the theory of sleep in much the same way as Duval, though he employs the term "morphological plasticity" instead of Duval's term "amoeboid movement." He cites researches on changes in functional variation and fatigue by Flesch, Magini, Vas, Lambert, Hodge, and Lugaro; but he lays particular stress on the researches of Mann and of Pergens. As these papers will be referred to again, no further notice will be taken of them here. Demoor points out Duval's misuse of Wiedersheim's observations and make a reply to Kölliker's criticism of the theory of amoeboid movements.

In 1896 appeared the thesis of Ch. Pupin (83) which the present writer has not had the opportunity of consulting. Duval says, however that Pupin (Pupin was his pupil) takes up the question chiefly on the theoretical side, and Deyber's paper, coming later, presumably embodies the essence of Pupin's generalizations.

During the same year other researches appeared from the hands of Ramon y Cajal (20 and 21) which have a bearing on the general

subject from the standpoint of the histology of the cortex. Another paper (22) the following year (1897) by the same author discussed again the function of the neuroglia.

In 1898 appeared the second and more elaborate paper of Duval (32) which covers about the same ground as Deyber's thesis. Duval says that when he suggested the hypothesis in his former paper the idea was already in the air, so to speak, ready to be formulated and he was the one to strike it off. At that time, he says, he was not aware of the previously published articles of Rabl-Rückhard (1890), of Tanzi (1893), of Lépine (1894).¹ The doctrine has now passed, he says, from the stage of an hypothesis to that of an anatomically demonstrated fact. He then refers to the work of his pupils. Two of them made the theory the subject of their inaugural theses. Pupin treats it on the theoretical side, while Deyber's thesis is an exposition of the researches of the two investigators, Demoor and Stefanowska. Still more recently another of his pupils, Manouélian, carried through researches in his laboratory which, he says, are clearly demonstrative of the truth of his doctrine. These researches will be taken up below. Duval cites van Gehuchten in support of his theory that there are certain regions, or a series of regions, where the peripheral articulate with the central neurones. The nuclei of the columns of Goll and of Burdach (posterior pyramids) in the medulla represent one of the more important of these regions. Here the peripheral pathways or neurones connect with the central, the axones of the latter passing to the cerebral cortex where they articulate with the dendrites of the pyramidal cells or psychical neurones. In sleep reflexes do not disappear. Consequently there is no interruption of the connections of the neurones which make up the reflex arc. The interruption in the case of sleep takes place either at the point of articulation of the peripheral with the central neurones or at the point of articulation of the central with the psychical neurones. But even these are not always completely interrupted as shown in the phenomena of dreams. Duval divides his proof, as does Deyber, into two main divisions, proofs by analogy and direct proofs. The proofs by analogy are the supposed amoeboid movements of the retinal elements on the one hand, and the supposed amoeboid movements of the olfactory cilia on the other. Deyber brings in also some collateral phenomena from other tissues. The direct proofs are found in the researches of Demoor, Stefanowska, Manouélian, and Odier. These will be taken up below in connection with the criticism

¹ He did mention Tanzi, however.

of Duval's evidence. Duval closes this paper with the statement of a fresh hypothesis which he calls the theory of *nervi-nervorum*.

Deyber's paper (30) also appeared in 1898. It appeared but two years after the thesis of Pupin. The publication of a second work on the same subject within so short a time was called out by the researches mentioned above, which contain the so-called direct proofs of the theory of Duval. One point peculiar to Deyber's treatment is his defence of the theory of contiguity against certain recent attempts to reestablish a doctrine of the continuity of the nerve elements, as exemplified by Dogiel. Duval's theory rests, of course, upon the assumption of the correctness of the current theory of the anatomic independence of the neurones. Deyber also makes a reply to Kölliker's criticism of Duval's theory. Deyber's paper winds up, like that of Duval, by referring to the large acceptance which the theory of amoeboid movements has had with histologists. Bechterew (11), van Gehuchten (39 and 50), Azoulay (6 and 7), Regnault (90), Le Dantec (56), Fleury (35 and 36) Richet (23) Soukhanoff (102 and 103), Querton (84), Loeb (60) all take a more or less favorable attitude toward it.

It may be seen, thus, from the foregoing series of papers, to what an extent this conception of the amoeboid contractility and expansibility of the neurone has penetrated the sphere of histology of the nervous system. The question now arises as to the interpretation of the evidence which has been presented. The aim has been simply to outline in a general way the historical development of the doctrine by reference to the chief papers which have appeared on the subject. Only articles which have taken up the subject with more or less fullness have been referred to here. Other articles will be referred to in what follows, which is a critical examination of the data presented.

II. CRITICAL.

We may follow Duval and Deyber and group the evidence into two general divisions, first, proofs by analogy, and second, direct proofs.

Before taking the first line of evidence, two points may be summarily disposed of—the supposed evidence from Wiedersheim's observations, and the argument from Tanzi. These cannot be proofs of the theory of amoeboid movement in any sense, since they are irrelevant to the point in question. Wiedersheim's observations (109) on the cerebral ganglion of *Leptodora hyalina* do not concern changes of the nerve cell as a whole, which alone can be characterized as amoeboid, but relate only to certain inclusions in the nerve cell which undergo

changes of form and position. This has been shown by the further researches on this crustacean by Samassa (95 and 96) and by Carlton (23). The same may be said regarding the inclusions observed by Svierczewski (105) and Freud (37). Tanzi's arguments (106) for the gradual approximation of the nerve branches by growth of the dendritic processes are doubtless in a general way correct, but they have no direct bearing on the question of such amoeboid movements as would be necessary to account for the relatively abrupt phenomena of sleep and awakening, association of ideas, memory, etc. The same remarks might be made with reference to the researches of Jacques (49) as cited by Deyber.

We pass to the proofs from analogy. The first of these proofs is found in general well-known cellular changes which take place under certain conditions in epithelial, glandular, and in cicatricial tissues. These tissues have all been studied with more or less care and with varying results for the purpose of demonstrating microscopical changes connected with their functional activity. Deyber includes under the term "amoeboid movement" all kinds of protoplasmic movements from those which botanists describe in the circulation of the protoplasm of plant cells to the oscillatory movements of the cilia of animal cells. To bring under the same name movements of such diverse nature seems a little forced, to say the least. But the study of the Protozoa has shown the existence, he says, of all gradations between what is ordinarily called amoeboid movement to the true vibratile ciliated cell. The researches of Schiefferdecker and Kossel (98) are cited. The presence of the amoeboid property is claimed also for the so-called myo-epithelial cells surrounding the sudoriparous tubes which are found in the external layer of the skin. Gland cells, says Deyber, exhibit movements during the process of secretion. The researches of Ranvier (86) on the salivary glands of the frog are cited. Reference is made to Ranvier (89) also for the changes which take place in the cells involved in the healing of a wound which, it is claimed, exhibit amoeboid movements.

In criticism it is to be said that in the cases of the epithelium and gland cells we are dealing with changes in the interior of the cell unaccompanied by alteration in the external form. In the case of the ciliated epithelial cells there is, properly speaking, no amoeboid property such as we find in the amoeba or leucocyte, but only a certain vibration of the fixed cilium. The changes cited in glandular tissue are obviously open to other modes of interpretation besides that of amoeboid movement. The reference to the myo-epithelial cells of the sud-

oriparous tubes is irrelevant, since in this case the contraction and expansion is in no way different from that in other muscular tissue. The difficulty seems to be that there is no definite criterion set up as to the meaning of the term "amoeboid movements." Going back to the typical case of the amoeba or leucocyte, it would appear that amoeboid movements must mean the extension and retraction of portions of the cell substance—an actual change in form and not merely of the interior parts of the cell. These changes are very different from those which are described as occurring in the case of the tissues mentioned above. True amoeboid movements mean changes in which the branches of the cell lengthen and shorten. The cells involved in the growth of cicatricial tissue are leucocytes, so that they furnish no *new* evidence for the theory. So far as it goes the evidence from the leucocytes, of course, is positive.

The next evidence is found in the facts concerning movements in the retina. These movements are claimed for two types of cells, first, for the pigmentary cells and for the rods and cones, and second, for the internal granular layer of bipolar cells and for the ganglionic layer of multipolar cells. Taking up first movements in the distal part of the retina, Deyber begins by referring to the researches of Boll (15 and 16) in 1877, who noticed that under the influence of light there was a change in the state of the pigmentary and rod and cone layers. These changes are interpreted as follows: Under the influence of light the pigmented pseudopodia of the pigment cells penetrate as far as the outer limiting membrane, while in darkness they retract, leaving unfilled spaces where they had been. Kuhne (53) made similar observations. Angelucci (2) in 1878 showed in the frog that the limit reached by the pigment in darkness was the external third of the rods. In 1884 he demonstrated that the pigmentary cell diminished in size under the influence of light, contracting in its width at the same time that the distal part of the rods became thicker. Angelucci himself believed this to be due to a migratory movement of the pigment within the cell. Van Genderen-Stort (41) observed, in 1884, a migration of the ellipsoids of the cones in darkness from their position next the outer limiting membrane to a position on a level with the external third of the rods. A little later, in 1887, he demonstrated (42) the contraction of cones under the influence of light. In 1885 Gradenigo (43) showed that the external granular layer undergoes changes. The nuclei in darkness become rounded; in light elongated. This is accompanied by a contraction of the internal part of the rods. In 1887 Denissenko (29) noticed that under the influence of light the entire

retina became thicker as a result of the enlargement of the space occupied by the external and internal granular layers. Mann (66) in 1894 in his researches on the dog discovered that the nuclei of the rods of the eye kept in darkness were diminished in volume and rich in globules of stainable substance situated in the periphery of the nucleus. On the other hand, after the action of light, this substance appeared concentrated toward the centre of the nucleus, presenting a star-like form. The recent experiments of Pergens (81), in 1896, confirm the work of Kühne, Angelucci and Gradenigo. His experiments were made on the eyes of a physostomous teleost, *Leuciscus rutilus*. Two lots of fishes were isolated, one in total darkness for 48 hours and the other in continuous light. At the end of this time they were killed and subjected to the same treatment. The figures that Pergens gives, as interpreted by Deyber, show that the pseudopodia of the pigment cells of the fishes that were kept in the dark are short, while in the other eyes the pseudopodia are long, penetrating deeply among the rods and cones. Along with this prolongation of the pigment cell is noted a contraction of the protoplasmic portion of the rods and cones. In the external granular layer Pergens found that the nuclei became elongated in darkness. Under the influence of light, on the other hand, there is a retraction of the protoplasm which re-enters in part into the external granular layer through perforations in the outer limiting membrane, Pergens also found movements in the internal granular layer of bipolar cells and in the ganglionic layer of multipolar cells in which the character of nerve cells is best preserved. Certain of the older investigators also found changes in this part of the retina, but their results are more or less conflicting. Since these changes are of the same character as those referred to below in the case of the true cortical neurones, no further citation of the researches is necessary.

Two criticisms may be made upon these results: (1) touching the argument in so far as it rests on the supposed movements of the pigment cells, and (2) the argument in so far as it rests upon the comparison of the tissues prepared in the light and darkness respectively. The second point involves the relation of the reagent used to the state of the tissue as affected by its activity. This will be taken up below. With reference to the first point, the sufficient reply to the argument, (in so far as these changes are not also amenable to the criticism which we are reserving until we come to speak of the neurone), in so far as it is based on changes in the pigment cells, is that recent researches render doubtful the inference that there is any true amoeboid movement in these cells. The fact is, as brought out for Crustaceans in a recent

paper by Parker (80) that the only change which has actually been observed here is a transfer or movement of the pigment granules *within* the cell, and no movement of the cell as a whole, such as Deyber assumes. The probability is that this is what occurs also in the higher forms. It will be recalled that this also was Angelucci's interpretation of his own results. As to the changes in the rods and cones, this evidence is good so far as it goes, and is certainly of more direct significance than that from the wandering leucocyte, since the rods and cones are more stable and fixed and thus more comparable with the cortical neurones.

The other proof by analogy cited by Duval and Deyber, that found in the olfactory epithelium cells, has been sufficiently met in what was said with reference to other ciliated epithelium tissue.

We pass now to the so-called direct proofs of the theory. These are found in what is interpreted to be evidence of amoeboid movements in the neurones themselves. A number of researches by different investigators on pathological states and on the effects of fatigue on the neurone are cited by Deyber and Duval as giving a histological basis for the theory. Deyber refers to the older researches of Remak, Heidenhain, Ranvier, Nussbaum, Ogata, Platner, Nickoläides and Mélenissos, and of Eeke. But he takes up in detail only the researches of the past fifteen years which are also the more conclusive in his opinion. In 1884, Flesch (34) in studying the Gasserian ganglion spoke of the migration of the nucleus outside of the cell body. Magini (64) in 1890 spoke of the displacement of a nucleolus in the motor nerve cells of the Torpedo after strong excitation, the nucleolus becoming in such a case eccentric, directed toward the axone, and enclosed by a heavy layer of karyoplasma. Vas (107) in studying the cervical sympathetic ganglion before and after excitation, showed, in 1892, that as a result of the irritation of the cell, the protoplasm became separated into two distinct zones, an internal and an external. The nucleus also took an eccentric position and the volume of the nucleus and of the whole cell underwent changes. Lambert (54) in his researches on the cervical sympathetic ganglion of the rabbit and young cat confirmed the results of Vas, except with regard to the changes in the cell volume. Hodge during the years 1889-1892 experimented on the spinal ganglion nerve cells of the dog, cat and frog. He found (46 and 47): A. For the nucleus: that fatigue is accompanied (a) by a marked diminution in the volume of the nucleus, (b) by a change from a smooth and rounded to a jagged irregular outline, (c) by a loss of the open reticular appearance with a darker stain; B. For the cell protoplasm: that fatigue is accompanied,

(a) by slight shrinkage of the protoplasm, (b) by lessened power to stain or to reduce osmic acid, (c) by vacuolation.¹ Andriezen in 1894 reported (1) on (the then unpublished) researches of Tuke and Mann which support the conclusions of Hodge. His own researches on changes in the nerve cells in the case of chronic alcoholism are also corroborative of the same conclusions. The work of Mann (66) followed immediately on that of Hodge. His researches on the sympathetic, motor and sensory nerve cells are important because he employed normal modes of stimulation. He shows that during the repose of the cell, the chromatin accumulates in the nucleus, while during the cell activity this stored-up material gradually disappears. The period of rest is accompanied by a turgescence of the protoplasm, of the nucleus, and of the nucleolus. In the fatigued cell the nucleus and nucleolus have a very sinuous outline, that is, as Deyber says, are very irregularly contracted. This is true also of the protoplasm. Further researches by Lugaro (63), by Ballet and Dutil (9), by Pugnât (82), by Marinesco (68 and 69), by van Gehuchten (39 and 40), by Nissl (73, 74, 75, 76, 77, 78), Soukhanoff (102 and 103), and by Stefanowska (104) are cited. The general conclusions are the same, except that Lugaro (63) maintains that it is the gemmules only which contract in different functional states, and that it is not their contraction but their expansion which is characteristic of sleep. The changes in the nerve cells which have been observed by these various investigators may be grouped under three general heads: (a) changes in the reaction to the stain, either as to the amount or the coloration of the stainable substance, (b) changes in the form or contents of the nucleus and nucleolus, (c) changes in the volume or character of the cell body. In the valuation of this evidence we must carefully distinguish between changes in form and changes simply in the contents or chemical reactions of the cells. The former only are relevant here.

In addition to the foregoing observations, certain researches showing changes in the dendrites and gemmules are regarded by Duval and Deyber as particularly convincing. Deyber first briefly states the arguments for the existence of the gemmules during life. He cites in support of his view Ramon y Cajal (17 and 18), Schaffer (97), Edinger (33), Azoulay (7), Monti (70 and 71), and Berkley (12 and 13). But it is upon the researches of Demoor, Stefanowska, and Manouélian that he bases his argument. Demoor (26) took three sets of dogs. He killed one by injection of morphine. Another, after being subjected

¹ This summary is taken directly from Hodge. For some reason Deyber's citation is very inaccurate.

to the morphine for some time, he killed by destruction of the medulla. Another dog he trepanned on both sides at the level of the crucial sulcus and allowed it to recover from the shock; the next day he took a small portion from the left hemisphere and then, after morphinization, he took a similar portion from the right hemisphere. All these pieces he treated in the same way. He found the cellular modifications identical in all these cases. Whereas in the normal animal before morphinization the terminal dendrites were covered with gemmules regularly distributed, in the operated animals these dendrites lost their gemmules. That is, according to Deyber's interpretation, these gemmules were retracted into the body of the terminal branches which bore them. But the retraction in the case of the operated animals was not confined to the gemmules, since the dendrites themselves took on a moniliform appearance. Such moniliform dendrites always ended in a terminal granule which was relatively large. If the morphinization was not so profound, the same results were discoverable, but were to be observed only in the finer ramifications of the dendrites. In another series of experiments Demoor trepanned the two sides of the head of a dog asleep with morphine. He then gave it liberty for thirty-six hours. At the end of that time he removed a piece from the left hemisphere and to the other side applied a strong electric current, immediately after which he excised a piece from that (the right) side. These pieces he treated in the same manner. The cells of the first piece were normal, that is, presented the gemmulated appearance and were not moniliform. In other words, the influence of the morphine was temporary only, producing a modification which disappeared during the thirty-six hours of repose. In the other piece, which had been subjected to the electric current, the cells were globular and very irregular in appearance as well as having their dendrites moniliform and granulated. In a subsequent paper Demoor (27) relates his observations to the theory of sleep, in somewhat the same way as Duval. Demoor (28) summarizes what he considers to be the significance of the moniliform state of the neurones for the theory of amoeboid movement as follows: (a) This moniliform state is indicative of a retraction of the protoplasm of the dendrites, (b) This retraction breaks the contact between the cellifugal and cellipetal ramifications of the neurones, (c) The nerve elements or neurones are plastic, and this property is of great significance from the point of view of their functioning and interconnections. A recent research by Hodge, undertaken with Goddard,¹ supports Demoor's con-

¹ This research is briefly reported in *Science*, N. S., Vol. IX, No. 217, p. 238.

clusions. Heger (44), also, arrives at similar results, though he finds that the three types of variation in the fatigued cells, changes in the cell body, in the dendrites, and in the gemmules, do not necessarily go together. Stefanowska's results (104), also, differ in no important respect from those of Demoor. Manouélian (67) undertook to carry out researches in which the facts dealt with should be more nearly normal or physiological results than those of previous investigators. To this end he brought about sleep through fatigue. He kept mice in a constant state of excitement until they feel asleep from sheer exhaustion. His results confirm those of the other investigators. Here, then, we have the data upon which is built up the theory of the amoeboid movements of the neurone.

We pass to the criticism of the use of these data as evidence in support of the theory of amoeboid movements.

In the first place, it is to be noted that it is by no means universally agreed among histologists that the gemmules represent prolongations of the living cell. Semi-Meyer (99 and 100) denies their existence as genuine structures and explains them as due to the Golgi preparations. Kölliker (52) takes much the same view.

The arguments for change in the position of the nucleus are more or less ambiguous. Similar alterations in form and even extrusion of the nucleus have been obtained in experimenting with the living amoeba. How much of this effect is due to the action of the reagents used remains to be determined. Hodge (48) has found similar contractions of the nucleus in the living cell as the result of normal fatigue. This shows that the observations above cited are certainly open more or less to the interpretation of Duval and Deyber. But as evidence for the theory of amoeboid movement the facts are not clear because of the lack of any criterion for what changes are due to the effect of the reagent and what are the normal result of fatigue.

No allowance is made in Duval's theory for the effects of the fixating reagents. Attention may be called to a paper by Professor Donaldson in the *Journal of Morphology* (Vol. IX, No. 1), entitled, "Preliminary Observations on Some Changes Caused in the Nervous Tissues by Reagents Commonly Employed to Harden Them." Professor Donaldson finds great changes in brain tissue under the influence of bichromate of potash in which there is an increase of weight and volume, and under the influence of alcohol in which there is a corresponding decrease in weight and volume.¹ Similar observations have been made

¹ This is but an example of the variations in volume caused by histological reagents in general.

on muscular tissue by Professor Loeb (59). Such facts show that a theory of movements of the protoplasm of the neurones can not be carried out without constantly interpreting the histological evidence in terms of the histological procedure.

The assumption underlying the theory of amoeboid movements, so far, at least, as the Golgi method is used, is that the substance of the cell in the living state extends as far as and no farther than the silver deposit which is continuous with the particular cell. The real question is as to just what the Golgi picture represents. No one supposes that the injection of the air-tubes and blood-vessels in insects by the silver-chromate stain represents exactly the nature of those tissues. Why should we assume that the nerve branches figured in the same sort of preparations actually occupy, down to the finest ramifications, all the places where you get the chrome-silver precipitate? In saying this, there is no desire to depreciate the value of the discovery of this method. Certainly we can see details here that no other method ever revealed. The question is as to the warrant in the use of *any* method for basing a physiological theory solely, or chiefly, upon small differences which may be due to the effect of the reagent alone.

The fact that fatigued or pathological cells show a different reaction from normal cells is not surprising. Naturally they would offer less resistance, to speak of nothing else, to the impregnating solution. This view is supported, moreover, by researches such as those of Heger (44) which show that contraction, varicosity, and the disappearance of the gemmules do not invariably coexist even in the case of stimulated or narcotized cells. Any one of these changes may exist independently of the others.

It is not the purpose of this article to attack the results of these investigators, but to show that there is this important point which cannot be overlooked, that the effects of the reagent have not been carefully discriminated from effects due to variations in the reaction of the cell according to its particular physiological condition. It is not denied that the neurones may possess an amoeboid property. It is simply denied that the evidence which has been confidently put forward in support of the theory, is wholly trustworthy as it has been employed. The real problem still remains, which is to demonstrate the existence of this property in the living tissue. It must be shown in some way which will obviate the effects of the reagents used, that there is an actual change in the spatial relations of the ultimate ramifications of the nerve cells.

Since the completion of this article there has appeared the abstract of a paper by R. Weil and R. Frank from the Pathological Institute of

the New York State Hospitals, to be published in the Archives of Neurology and Psychopathology, Vol. II, Nos. 3-4, 1900. It is entitled "On the Evidence of the Golgi Methods for the Theory of Neurone Retraction." The general conclusions support the position taken in the present article. They are as follows:

"I. The same material, when treated by different methods, yields different results. The nature of the differences in case of each kind of material is as follows:

"All material treated according to the slow method of Golgi, shows, as a rule, an almost absolute freedom from varicosities; varicose cells occasionally occur, but with relative frequency which is perhaps not greater than a fraction of one per cent of the total number of pyramid cells impregnated. Exceptionally, a large proportion of varicosities occurs.

"The mixed method and the rapid method may be considered together; these two methods yield practically similar results as regards the varicosities and the gemmules. The gemmules are almost invariably present and generally regular, provided the dendrites have taken impregnation. The varicosities occur in variable proportions, although their frequency regularly is greater, and almost always very much greater, than is the case in the slow method. In some sections, almost every dendrite is varicose, in others, hardly any.

"In the Cox method, a fair amount of varicoseness is generally present at any stage of fixation. Gemmules are almost universally present and regular.

"II. The above results are independent of the nature of the material, whether normal or toxic. Normal material, as well as toxic, is, as a rule, free from varicosities when treated by the slow method. Normal material, as well as toxic, exhibits a variable amount of varicosity, when treated by any of the other three methods which we have used. We find that it varies within exactly the same limits as the abnormal, that every degree of varicoseness can be illustrated with equal freedom from either, and, finally, that it is impossible for an unprejudiced observer to differentiate or distinguish between the two kinds of material.

"III. The same material does not yield constantly identical results, when treated by one and the same method. Pieces from the same animal, when immersed in the same fluids of the slow, mixed, rapid, or Cox method, may illustrate the extreme of varicoseness produced by that method.

"The above conclusions seem to demonstrate that the varicosities are to be regarded as artifacts of the Golgi method."

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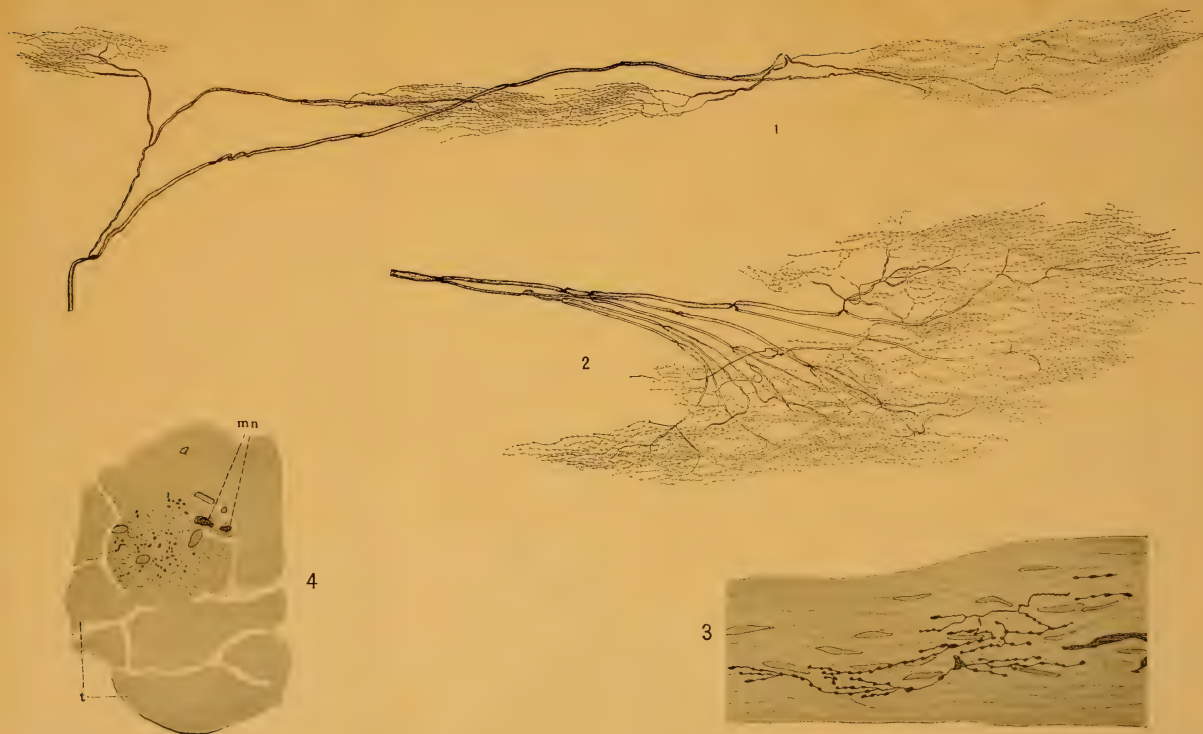
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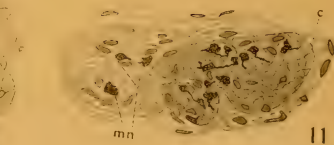
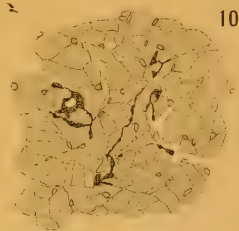
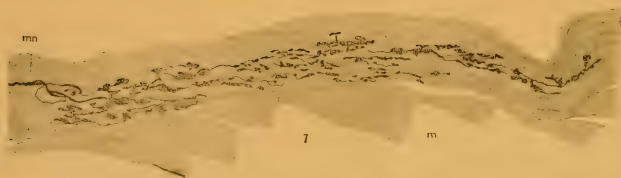
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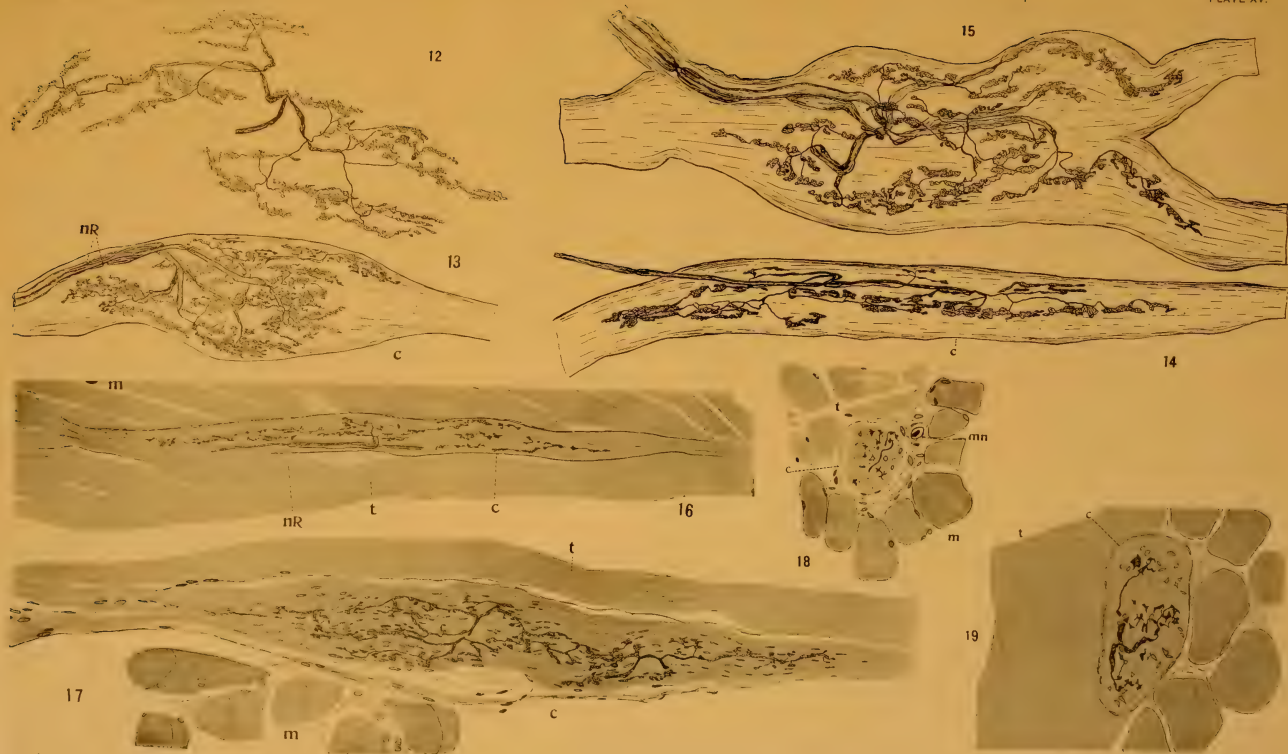


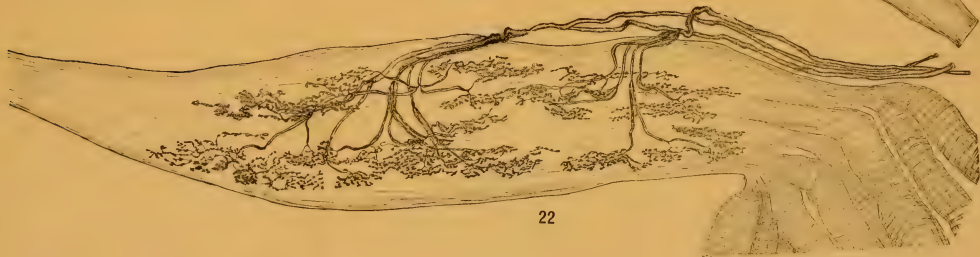
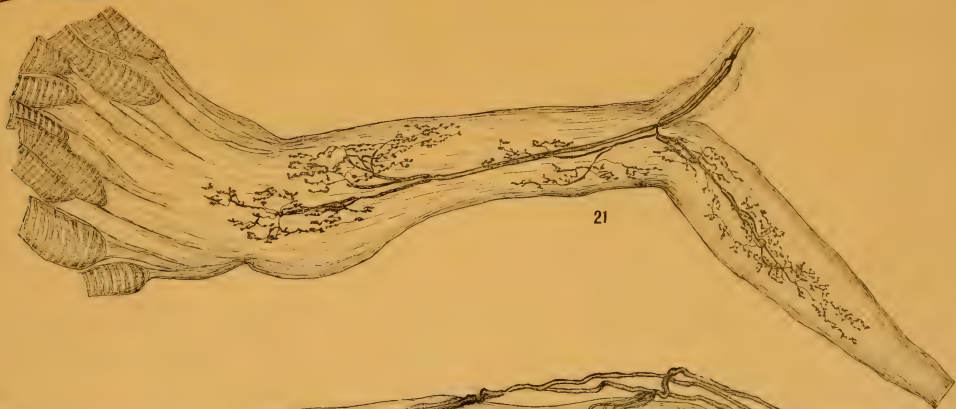
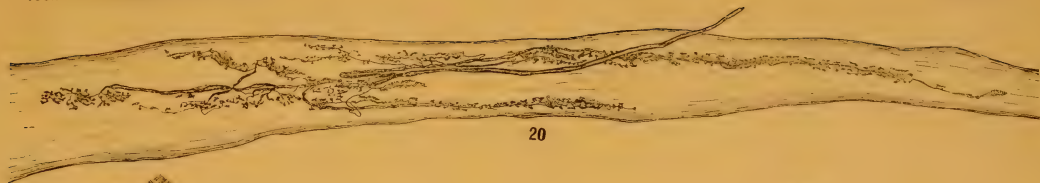


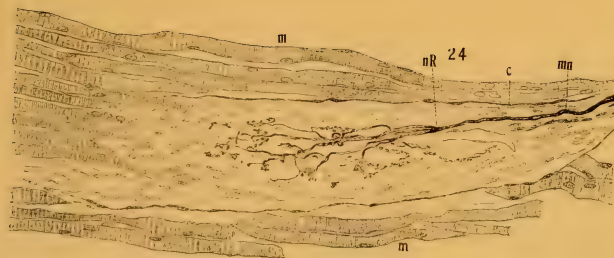
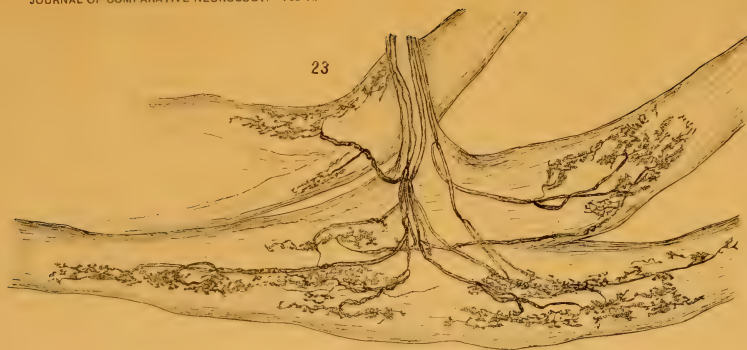


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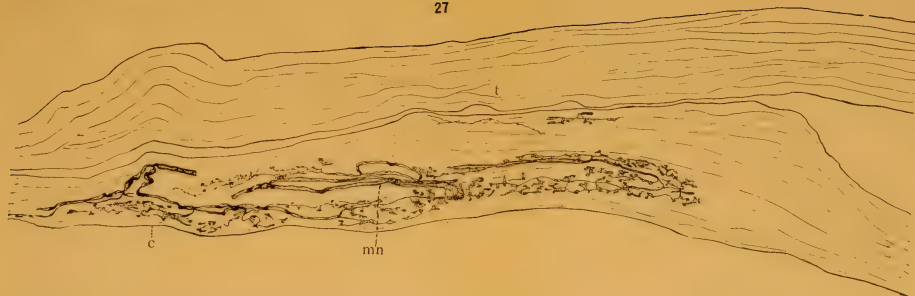
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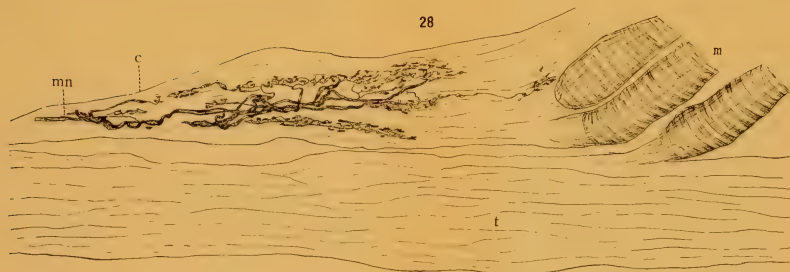




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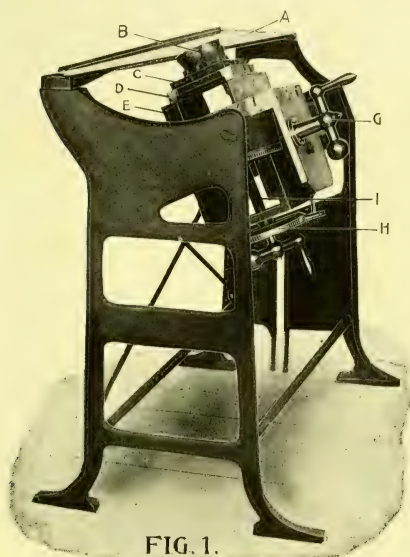


FIG. 1.

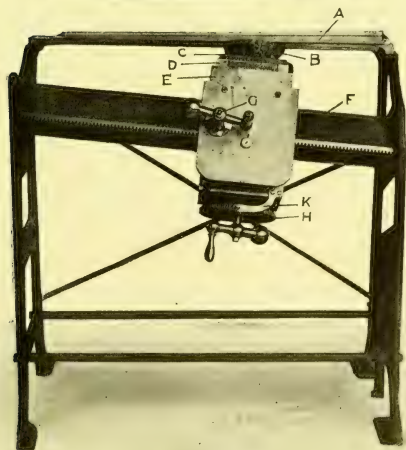


FIG. 2



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A CONTRIBUTION UPON THE CRANIAL NERVES
OF THE COD FISH.

By C. JUDSON HERRICK.

With Plates XXI and XXII.

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I. INTRODUCTION.

The nerves of the cod fish have been so often dissected and described that one would think that further contributions on this subject would be superfluous. Nevertheless even the most recent of these descriptions leaves some of the most essential matters in this connection to a large extent obscure, viz.

the exact courses of the several nerve components through the ganglionic complexes. Even Cole, whose researches on the nerves of fishes are in many respects the most valuable which we have had since Stannius, was only partially successful in his analysis of these complexes.

In the course of the final revision for the press of my previous contribution upon the peripheral nervous system of *Menidia* I received Cole's memoir on the nerves and lateral line system of the cod, to which reference has just been made. I was pleased to find a close agreement between his conclusions and my own in most important respects. There were, however, some points of difference, not only in the theoretical deductions to which we were led by our facts, but in the basal facts themselves—differences which could be explained only on the assumption either of erroneous observation on the part of Cole or myself or of differences in the structure of the two fishes under consideration which would be most unexpected in view of their rather close relationship.

These discrepancies are in some cases important, not as mere matters of anatomical detail, but because of their broader application to the theories of nerve components, upon which I was at that time especially engaged. I therefore determined to examine some points in the structure of the peripheral nerves of the genus *Gadus* myself.

The differences between Cole's results and my own are almost altogether such as can be cleared up only by the microscopical analysis of the nerve roots; I therefore employed in the main the same methods as those used in the research upon *Menidia* already referred to; viz., the preparation of serial sections of small fish, hardened entire in Flemming's fluid and stained by the Weigert method. The young specimens of *Gadus morrhua*, about 7 cm. long which were sectioned in this way were dredged for me in Vineyard Sound by Mr. Vinal Edwards of the Woods Hole Station of the U. S. Fish Commission during the summer of 1898; the sections I prepared, with the assistance of my pupil, Miss Laura B. Moore, in the Zoological Laboratory of Denison University; and the micro-

scopical study of these sections was conducted mainly in the Fish Commission Laboratory at Woods Hole during the summer of 1899. This work was, moreover, controlled by the dissection of various species of gadoid fishes made at the same time by my assistant, Mr. E. C. McKibben.

Attention was especially directed to the trigemino-facial complex, and these roots, together with the proximal courses of the rami, have been carefully plotted. In order to give to the reader some of the more important data upon which the plot is constructed a series of transections through this complex is also figured. Our dissections have shown, what previous workers have found, that the gross method is quite inadequate to unravel the intricate mesh of fibers and ganglia presented by such a root complex, and Cole's results have also shown that the microscopical method is also inadequate unless the conditions are especially favorable. He states that his sections did not permit a complete analysis of the complex, and suggests in another place that some of the details could be made out only by the careful study of good Weigert sections—a point in which I quite concur. I think that I have had somewhat better success in this analysis than my colleague, and submit the following general results of a comparison of my findings with his:

1. In general there is a very close agreement in the peripheral nervous systems of *Menidia* and *Gadus*, even down to rather trivial details—closer than would be supposed by a comparison of my *Menidia* paper with Cole's *Gadus* paper.

2. There are a few structural differences between the two fishes which are of considerable importance.

3. I am, however, forced to conclude that there were some defective and some erroneous observations on Cole's part, due apparently, to the limitations of his methods of research.

4. And, finally, there are a few cases growing out of the latter point in which I must take issue with Cole's morphological interpretations.

This work has been done on the basis of my previous analysis of the components in *Menidia* and, as stated above, by the same methods. To avoid repetition I shall therefore throw

my results to some extent into the form of a comparison with *Menidia*. For the same reason I shall refer the reader to that work so far as possible for bibliographical and critical details.

The nomenclature of the nerves presents the same difficulties here as in *Menidia*, difficulties arising not only from the diverse names given by different authors to the same nerves, but especially from the fact that with but few exceptions the nerve roots as ordinarily enumerated do not bear any simple relation to the trunks and rami which arise from them. As a rule, therefore, the peripheral nerves do not correspond to the roots which bear the same names and numbers, but fusions and anastomoses of the most puzzling kind occur everywhere. The result is that, so long as the present unphilosophical nomenclature is employed, it often happens that a given peripheral ramus containing several components must be assigned to one of two or three cranial nerves upon purely arbitrary grounds. The criterion most often appealed to here is priority or anatomical authority, with results which are not always permissible. For instance, the communis fibers which go out with the supra-orbital trunk in some fishes are usually reckoned as part of the ophthalmicus superficialis V, instead of the r. ophthalmicus VII, although it is now definitely known that these fibers arise from the geniculate, or facial ganglion. As a matter of fact it is unphilosophical to ally them with either the general cutaneous trigeminal fibers or the lateralis facialis fibers. This communis nerve should have a name of its own. The time is rapidly approaching when we shall have a sufficiently detailed knowledge of the composition of the cranial nerves throughout the Vertebrata to make it possible to construct a typical schema for the nerves of the vertebrate as a whole. And until that time comes matters of nomenclature should be left in abeyance. I shall therefore use in general the same names for the nerves as in the *Menidia* paper, conforming as far as possible to conventional usage.

Most of the motor nerves have been worked out, but as they conform to previous descriptions and have no direct appli-

cation to the morphological problems which underlie this study, I shall not dwell upon them except in a few cases.

II. DESCRIPTIVE PART.

1. *The Trigemino-facial Complex in General.*

As compared with *Menidia*, the trigemino-facial complex is very compact. The ganglia, except the sympathetic, are almost entirely intra-cranial and they are all crowded together into a single subspherical mass. I merely summarize the experience of previous workers, as well as my own, when I say that the method of dissection is totally inadequate to resolve the intricacy of this entanglement of fibers and cells. Indeed I doubt if I could have been sure of the real meaning of some of my microscopical findings if I had not had before me the simpler paradigm given by *Menidia*. Nevertheless, in spite of the greater apparent intricacy thus introduced, the complex in *Gadus* reduces to a type almost exactly like that of *Menidia*.

Thus, the Gasserian ganglion, though intra-cranial, is in all other important respects similar and it gives off the same general cutaneous nerves as in *Menidia*. The geniculate ganglion is much more intimately joined to the Gasserian in *Gadus*, but gives off communis branches in the same way except that this component is absent from the truncus hyomandibularis, but present in the r. mandibularis V. The lateral line roots, ganglia and nerves are as in *Menidia*, save for much greater compactness, so that the dorsal and ventral lateral line ganglia are only imperfectly separated. All of the rami arising from this ganglionic complex except the supra-orbital trunk and the r. recurrens facialis, or facial root of the r. lateralis accessorius, emerge from the cranium by a common foramen. We shall now review the course of each component through the complex.

2. *The Lateral Line Roots of the Facialis.*

This component lies external to all of the other members of the trigemino-facial complex and is the easiest to analyze. The two lateralis roots emerge from the oblongata together and in very close relations on the ventral side to the great auditory

root. The communis and motor VII roots emerge at the same transverse level and in about the same relations as in *Menidia*. The dorsal and ventral lateralis roots do not separate at once, but run forward together until the level of the origin of the trigeminus root is reached. Ganglion cells appear scattered through both dorsal and ventral portions far caudad of this point, so that the dorsal and ventral lateralis ganglia can be only imperfectly separated. Ganglion cells, however, extend out a short distance into the rami beyond their separation.

The communis root emerges mesially of the dorsal portion of the lateralis roots, but soon comes to lie in the notch between the dorsal and ventral roots, from which, however, it is at once crowded ventrad by the emerging trigeminus. As soon as the two lateralis roots separate, the motor VII root is pushed in between them, lying laterally of the trigeminus root and of the dorsal edge of the communis root (Fig. 3).

The ventral lateralis root enters the truncus hyomandibularis in the way typical for teleosts, turning sharply ventrad and emerging from the cranium at once after separating from the dorsal root. The dorsal lateralis root, after separating from the ventral, continues cephalad a short distance, the motor VII and the sensory V roots crowding in between the two lateralis roots as already mentioned. A small root of the r. lateralis accessorius (*rec. 3*, Fig. 1) also passes between them in this region, as will be described beyond. The dorsal root divides a short distance beyond the ganglion into the r. buccalis and the r. ophthalmicus superficialis VII in the usual manner. The former gives off at once the otic and outer buccal nerves and then turns ventrad with the infra-orbital trunk. The latter continues cephalad in the original relations, forming a part of the supra-orbital trunk. The courses of these nerves through their trunks will be described below.

3. *The Communis Root of the Facialis.*

The fasciculus communis root of the facialis pursues its intra-cranial course and terminates in the lobus vagi essentially as in *Menidia*, though it is considerably larger in *Gadus*. The

fasciculi of the two sides run back as close to the median line as possible, practically in contact with each other under the fused tubercula acustica and immediately over the fourth ventricle, whose lumen is constricted in this region to a very narrow tube. The glossopharyngeus does not enter the fasciculus communis, but its sensory fibers enter the lobus vagi in intimate relations with those of the vagus.

The origin of the communis root from the oblongata has already been described. It is at once crowded ventrally between the brain and the lateral line and motor VII roots. The most dorsal fibers of the communis root run forward after the separation of the dorsal and ventral lateralis roots in the notch between these roots (Fig. 3) lying laterally of the trigeminus root. From this point a continuous band of communis fibers runs down the inner face of the ventral lateralis root and in this latter region the cells of the facial (geniculate) ganglion first appear.

This ganglion is large and wholly intra-cranial, occupying the space ventrally and mesially of the ventral lateralis root. Farther cephalad some cells of this ganglion are wedged in between the ventral lateralis and motor VII roots ventrally and the V and dorsal lateralis roots dorsally (Fig. 4). From the latter cells the third rootlet of the facial root of the r. lateralis accessorius arises, as described below.

The geniculate ganglion terminates in front rather abruptly. A narrow tongue of cells runs farther forward dorsally and from this the very slender communis component in the supra-orbital trunk arises. Ventrally the ganglion is produced into the bundle of communis roots which leave the complex in connection with the infra-orbital trunk or behind it. This bundle includes all the communis nerves of the facialis except the roots of the r. lateralis accessorius and the fibers for the supra-orbital trunk. It runs forward under the infra-orbital trunk and the big blood vessel lying internally of the latter (orbital vein), over the first sympathetic ganglion and externally of the VI nerve (Fig. 7).

The palatine nerve separates from the mesal side of this bundle and emerges from the cranium farther forward with the

infra-orbital trunk closely wedged in between the sympathetic ganglion and the VI nerve. Closely associated with the palatine at its origin is a large bundle of communis fibers which joins the r. maxillaris V intra-cranially and another which joins the r. mandibularis V. The other communis fibers pass ventrally to go out through the foramen between the exits of the truncus hyomandibularis and the infra-orbital trunk. The space between these trunks in the foramen and just external to it is occupied by the first sympathetic ganglion of the "head part" of the sympathetic chain. All of these communis fibers, therefore, have to pass either through or close around this large sympathetic ganglion in passing out of the cranium. They also pass out very closely joined to the motor fibers of the r. opercularis profundus VII for the mm. adductor arcus palatinus and adductor hyomandibularis (Figs. 6, 7). A short distance beyond the foramen they separate into the r. pre-trematicus VII and the Jacobson's anastomosis.

4. *The Trigeminus Roots.*

The intra-cerebral and root portions of this nerve are, so far as observed, exactly as in *Menidia*. The ganglion, however, is much less distinct, and crowded back farther toward the brain and squeezed in among the other roots. It is largely intra-cranial, but a considerable proportion of it lies in the foramen or just outside. As the root is followed outward cells of the Gasserian ganglion appear first on the lateral and ventral side of the root (Fig. 6). These lie close to those of the geniculate ganglion, but farther laterally and dorsally, as well as farther cephalad, and in favorable preparations there is no difficulty in distinguishing the boundaries of the two ganglia. If, however, the sections were not in every way favorable, it would probably be by no means easy to distinguish them, for their cells are of almost the same size and they are separated by only a narrow zone of fibers.

These cells are closely crowded in between the trigeminus root and the ventral lateralis root as it curves back into the hyomandibular trunk. A little farther forward the ganglion

expands to fill the space between the origins of the hyomandibular trunk and the infra-orbital trunk, and still farther cephalad this latter portion of the ganglion bulges out through the foramen and over the origin of the infra-orbital trunk, thus forming the extra-cranial portion of the ganglion (Fig. 7). Meanwhile ganglion cells have appeared throughout the root and this more mesal portion of the ganglion continues forward a short distance into the supra-orbital trunk (Figs. 8, 9).

The relations of the trigeminal rami present no points of morphological difficulty. A considerable number of general cutaneous fibers is given off from the extra-cranial portion of the Gasserian ganglion which accompany the otic and outer buccal nerves to the skin near the lateral line organs which these nerves supply (Fig. 7, *r. ot. cut.*, Fig. 8, *out. buc. cut.*). Neither these two general cutaneous nerves, nor the one next to be mentioned are figured on the reconstruction, Fig. 1.

From the intra-cranial portion of the Gasserian ganglion the *r. ophthalmicus superficialis V* arises and most, if not all, of the *r. maxillaris V*, while the *r. mandibularis V* arises chiefly from the extra-cranial portion of the ganglion. The origins of the *r. maxillaris* and *r. mandibularis V* are essentially as in *Menidia*, except that they separate from each other sooner, i. e., the *truncus infra-orbitalis* is very short.

5. *The Motor Facialis.*

The course of the motor V fibers through the ganglionic complex is implied in the account of the trigeminus root above. The motor VII should receive a more detailed mention, since there is reason to believe that some of these fibers have been recently interpreted incorrectly.

The root may be traced from the *fasciculus longitudinalis dorsalis* out to the hyomandibular trunk almost exactly as in *Menidia*. It is about as large as in *Menidia* and takes the same course, running through the dorsal part of the spinal V tract and applying itself to the inner face of the compound lateral line root of the *facialis* (Fig. 2). As the ventral *lateralis* root separates from the dorsal, the motor VII swings up and occu-

pies the dorsal side of the ventral lateralis root, being bounded mesially by the communis root of the facialis and dorsally by the dorsal lateralis root (Fig. 3).

Now, as the ventral lateralis root passes through its foramen in the cranium, the motor VII swings down along its inner face (Fig. 5) and in the foramen divides into two unequal portions. The smaller one runs along the ventral and caudal face of the emerging lateralis root, then caudad along the dorsal and outer face of this root, leaving it, however, as soon as the hyomandibular trunk turns cephalad. This portion constitutes the branch of the r. opercularis profundus VII for the mm. levator and adductor operculi (Figs. 5 and 4, *r. op.*). It runs back internal to the hyomandibular bone, running along the dorsal face of the pseudobranch, following parallel to the opercular process of the os hyomandibulare and dorsally of it, to its muscles. It is a very minute nerve, carrying a few coarse fibers.

The larger portion of the motor VII turns ventrad from the hyomandibular foramen (Fig. 6, *r. add.*) and contributes most of its fibers to the branch of the r. opercularis profundus VII for the mm. adductor arcus palatini and adductor hyomandibularis. These muscles lie under the foramen and the nerve spreads out among them at once, one branch running far cephalad along the dorsal surface of the m. adductor arcus palatini as far as that muscle extends (Figs. 7, 8, 9, *r. ad. pal.*). This nerve at its origin is very closely joined to the communis nerves for the r. pre-trematicus VII and Jacobson's anastomosis.

6. *The Supra-orbital Trunk.*

This trunk is composed very nearly as in *Menidia*, with large lateralis and general cutaneous components and a very small communis element. The trigeminal and facial superficial ophthalmic nerves are quite intimately joined for most of their courses and the few communis fibers are mingled with those of the r. ophthalmicus superficialis V.

The two superficial ophthalmic nerves do not pierce the cranium with the others of the trigemino-facial complex, but

run forward for a long distance in a sheath of connective tissue lying in the membranous cranial wall mesially and later ventrally of the ventral tip of the supra-orbital cartilage. Still farther forward they run intra-cranially under the supra-orbital canal, which lies in the lateral edge of the frontal bone.

I confirm Cole's account of the peripheral course of the r. ophthalmicus superficialis VII.

From the dorsal tip of the geniculate ganglion an exceedingly minute twig of communis fibers runs forward and over the trigeminus root (Figs. 6 to 9, *com. oph. sup.*) to take a position in the extreme dorsal part of the Gasserian ganglion close under the r. ophthalmicus superficialis VII. Here it continues cephalad along the dorsal edge of the r. ophthalmicus superficialis V until this nerve gives off its first branch. It is impossible to be certain of the course of these fibers; but it appears from the sections that most of these fibers enter this first branch.

Immediately cephalad of the Gasserian ganglion the r. oph. sup. V sends a large branch outward, mentioned just above, which pierces the membranous cranial wall under the supra-orbital cartilage, then turns dorsad and cephalad along the outer side of this cartilage. This position, however, it soon leaves, turning laterally to spread out in the tissues over the eye-ball and in the overlying skin. One large twig runs down upon the cornea. Another runs forward parallel to the main nerve where over the middle of the eye it joins a branchlet of r. oph. sup. VII destined for pit-organs and derived from the nerve for supra-orbital canal organ 5.

The observations upon the communis component of the supra-orbital trunk could not be controlled on the opposite side of this fish. The number of these communis fibers is so small that their exact course is not a matter of great importance. It is clear from this reason alone that they supply no considerable number of terminal buds anywhere, and it is quite as probable that they are of general visceral nature and do not go to the skin at all.

At the level of the last (5th) supra-orbital canal organ a

small twig leaves the r. oph. sup. V and runs dorsad along the inner side of the r. oph. sup. VII. When the nerve for the fourth canal organ enters the canal through its foramen, in the frontal bone, this nerve accompanies it and passes directly up through another foramen in the roof of the canal to distribute to the skin over the canal cephalad of the fourth organ and of the supra-orbital commissure.

A very little farther cephalad a similar twig leaves the r. oph. sup. V, which runs dorsad along the outer side of the r. oph. sup. VII and distributes in several minute branchlets to the skin over the cephalic part of the orbit, one running out upon the cornea. Other similar twigs follow as we pass cephalad, one large one in the anterior part of the orbit.

The main nerve spreads out to the skin of the top of the snout about the cephalic end of the supra-orbital canal, remaining in very intimate union with the r. oph. sup. VII until that nerve sends its last large branch to supply the first supra-orbital organ. Indeed the association of the two nerves is continued beyond this point, as the terminal twigs of the r. oph. sup. V are accompanied by facialis fibers for the pit-organs of the top of the snout.

7. *The Hyomandibular Trunk.*

The truncus hyomandibularis, as in *Menidia*, receives the whole of the ventral lateral line root, which composes the r. mandibularis externus VII, and a band of general cutaneous fibers from the Gasserian ganglion, but it receives no communis fibers from the geniculate ganglion, so that it lacks the r. mandibularis internus VII.

The general cutaneous component arises from the extracranial portion of the Gasserian ganglion as a moderately large nerve which runs outward, downward and backward to enter the hyomandibular trunk. This agrees in every way with the corresponding nerve in *Menidia* except that it is larger in *Gadus*, is single rather than double and passes more directly into the truncus.

Fully one half of these general cutaneous fibers go out at

once with the combined r. opercularis superficialis VII and r. hyoideus and distribute to the skin of the lower part of the operculum. The remainder continue in the hyomandibular trunk to the cephalic and ventral edge of the operculum, where they also distribute to the skin. None of them accompany the truncus into the mandible.

The motor VII branches which constitute the r. opercularis profundus have already been described. The second nerve to leave this trunk is the large mixed nerve referred to in the preceding paragraph, which from its course is clearly a fusion of the r. opercularis superficialis VII and the r. hyoideus VII, as I applied these terms to *Menidia*. It contains motor, general cutaneous and lateralis fibers, and leaves the trunk immediately upon its exit from its foramen. As the trunk turns cephalad this nerve separates from it (Fig. 1, *op. s. + hy.*), passing outward along the cephalic face of the hyomandibular bone to run caudad and ventrad along the outer surface of this bone between it and the m. adductor mandibulæ, and farther back between this muscle and the pseudobranch.

Just behind the hyomandibular bone, as this ramus runs down along the inner face of the m. adductor mandibulæ, it gives off a minute twig of coarse (lateralis) fibers which retains its position in the dorso-mesal edge of the muscle to its caudad end. This little twig (Fig. 1, *r. o. p. l.*) follows the posterior and ventral borders of the operculum, turning cephalad again along the ventral border below the opercular canal and overlying the course of the r. hyoideus. Pit-organs are frequent in the skin along its entire course and fibrils from it were in several cases traced to these organs. It probably contains no general cutaneous fibers, as the corresponding area of skin has an independent innervation with finer fibers. This twig was apparently overlooked by Cole. A larger coarse-fibered twig is given off at the same time as the last. It supplies the last, or 12th., operculo-mandibular canal organ.

The mixed opercular and hyoideus nerve then runs down along the inner side of the pre-opercular and inter-opercular bones close under the mucous lining of the operculum. It

sends a twig of the coarse fibers to supply the 11th organ of the operculo-mandibular line and from this point may be regarded as containing the r. hyoideus only (Fig. 1, *hy.*).

Having reached the ventral edge of the operculum, it divides, one portion turning caudad and a larger portion cephalad and both containing both coarse and fine fibers. Neither portion distributes to cutaneous sense organs of any description; the distribution shows that the finer fibers are general cutaneous and the coarse fibers motor. The caudal branch of the r. hyoideus enters the branchiostegal membrane and supplies its skin and muscles behind this point. The cephalic branch runs along the ventral edge of the operculum mesially of the interoperculum, ventrally of the cerato-hyal and just dorsally of the line of attachment of the branchiostegal membrane, in which position it gives off frequent branchlets of coarse and fine fibers which distribute to the skin and muscles of the branchiostegal membrane like the branch last described. It distributes forward in the branchiostegal membrane to its cephalic end. A few fibers are also distributed to the skin covering the cephalic end of the interopercular bone. This nerve (the r. hyoideus) anastomoses in front with the branches of the r. mandibularis V for the genio-hyoideus muscle, as in *Amia* (Allis, '97).

After the separation of the combined superficial opercular and hyoideus nerve, the next branch given off from the hyo-mandibular trunk is the lateralis branch for pit-organs, the nerve H' of Cole (Fig. 1, H'). This nerve runs laterad and cephalad between two slips of the m. adductor mandibulæ and farther cephalad between the ventral one of these slips and the ventral edge of the m. levator arcus palatini. Still farther cephalad, under the eye, this twig bends outward across the dorsal side of the m. adductor mandibulæ to reach the skin, in which it distributes in many minute branchlets terminating in pit-organs. These organs lie chiefly in the area of skin under the eye between the infra-orbital and mandibular canals, but also farther back upon the operculum over the opercular canal, and one twig runs cephalad onto the mandible to supply a row of similar organs lying along the mandibular canal for almost its entire

length. Both Allis and Cole have described this nerve correctly. Not all of its twigs were traced to sense organs (the skin being defective in places), but this is probably the mode of ending of all of them, as this area of skin has an independent general cutaneous innervation.

Following the nerve last described, branches are given off from the hyomandibular trunk for the canal organs 10, 9 and 8 of the operculo-mandibular line, as figured by Cole. The next nerves to leave the trunk are three fine fibered twigs which apparently include all of the remaining general cutaneous fibers of the trunk. These distribute to the skin of the ventro-cephalic edge of the operculum.

The trunk then enters the lower jaw and runs forward along the inner side of Meckel's cartilage in the manner typical for teleosts. Unlike *Menidia*, however, the truncus here appears to contain only lateralis fibers, i. e., it consists only of the external mandibular nerve, the communis fibers constituting the internal mandibular nerve not being present in this fish. The nerve, as seen in cross sections, is composed of coarse and medium fibers, the former scattered irregularly among the latter and all very densely myelinated. There are a very few quite small fibers among them, but these are not segregated into a compact fascicle, as general cutaneous or communis fibers generally are when they accompany lateralis fibers, and besides, though small, they are heavily myelinated.

The peripheral relations of the truncus hyomandibularis have been carefully worked out. I find that they correspond closely to Cole's descriptions, which I confirm in every important respect. There would seem to be great individual variability as to the precise courses of the several nerve trunks running in the mandible, even on opposite sides of the same specimen. Yet these variations are of small morphological importance.

8. *The Infra-Orbital Trunk.*

The truncus infra-orbitalis is composed about as in *Menidia*. It breaks up into its component rami earlier in *Gadus*

and these rami are somewhat differently composed. It receives, as in *Menidia*, the ventral division of the dorsal lateralis root (*r. buccalis*), the whole of the motor V root, the larger part of the general cutaneous fibers from the Gasserian ganglion and a considerable number of *communis* fibers from the geniculate ganglion. The motor V fibers run out in the midst of the sensory V, from which they can be distinguished by their larger caliber. The *r. buccalis* occupies the dorsal part of this complex and the *communis* component the ventral. The relations of the components as the trunk passes through its foramen are shown in Fig. 7.

Just outside of the foramen the trunk divides into three approximately equal divisions, the *r. maxillaris*, the *r. mandibularis V* and the *r. buccalis*. The motor V fibers clearly go out with the *r. mandibularis*. The *communis* fibers from the geniculate ganglion could not be so clearly followed, as they divide up into several fascicles which interlace with the general cutaneous fibers from the Gasserian ganglion. *Communis* fibers can, however, be seen to enter both the *r. maxillaris* and the *r. mandibularis V*.

The r. buccalis.—I have followed this nerve for its entire length in my sections, but can add little to Cole's account of it. The otic and outer buccal nerves are, as stated above, accompanied by general cutaneous fibers, corresponding, as Cole has mentioned, to nerves in the same relation in the tadpole of the frog (Strong, '95) and in *Amia* (Allis, '97). One of these twigs was traced forward onto the cornea. A minute twig is given off from the outer buccal nerve between the 7th and 8th infra-orbital canal organs for naked pit-organs ventrally of the latter organ (Fig. 1, *b. p. o.*). These organs lie caudad and dorsad of those supplied by the branch H⁷ of the hyomandibular trunk.

I confirm Cole's account of the course of the inner buccal branch completely; the only differences which I find are in the branches to the pit-organs about the infra-orbital canal and these slight differences do not seem to be of any morphological importance, but rather matters of individual variation. Most

of these twigs for pit-organs are accompanied by general cutaneous fibers; sometimes these join the lateralis twigs at once upon their separation from the buccalis, sometimes they apply themselves to these twigs later. The general cutaneous supply of this region comes from the r. maxillaris.

The curious nerve which Cole describes ('98, p. 158) from the r. buccalis to a pit-organ near the cephalic end of the supra-orbital canal I also find and verify his description. I have already commented ('99, Sec. 7, VII, 6, at end) upon Cole's interpretation of this nerve and shown evidence that it is a nerve of rather wide occurrence among the fishes.

The r. maxillaris is composed of fine fibers with a few very coarse ones and a larger number of medium size scattered among them, an arrangement which is characteristic of general cutaneous nerves. We have seen that this nerve also receives a communis element from the geniculate ganglion.

It runs forward under the eye as a compact bundle internal to the r. buccalis and internal and dorsal to the r. mandibularis V. Upon the separation of the r. mandibularis to enter the lower jaw the r. maxillaris retains its former relation to the r. buccalis. In this part of its course it gives off no branches. In the cephalic part of the orbit (at about the level of the fifth supra-orbital canal organ) it breaks up into several branches of unequal size, of which one passes out laterally between the upper and lower inner buccal branches and distributes to the skin of the cephalic border of the orbit. The other bundles into which the r. maxillaris divides in the cephalic part of the orbit are (1) the largest one, lying farthest mesially; (2) one somewhat smaller, lying dorsally; and (3 and 4) two very small ones ventrally, all running very close together for a considerable distance. The smaller ventral branch (4) passes to the skin of the snout just dorsally of the maxillary bone. The larger of the two ventral branches (3) runs down farther cephalad into the skin overlying the maxillary bone about the posterior angle of the gape. The dorsal one (2) in front of the orbit under the nasal sac applies itself closely to the inner face of the upper inner buccal branch, and the fibers of the two nerves interlace

more or less. Part of these fibers distribute to the skin along with the branches of the r. buccalis destined for the pit-organs under and in front of the nasal sac. The remainder of the fibers of the second branch accompany a few buccal fibers for pit-organs about the extreme cephalic end of the supra-orbital canal. They distribute to the skin of the same region and farther caudad. The branch (1) goes forward to the tip of the snout without giving off any branches. It then passes through the premaxillary bone. Some of its fibers enter the alveolar canal of this bone and doubtless supply its teeth, while the greater part distribute to the upper lip and the terminal buds with which it is plentifully supplied. It is clear, therefore, that this branch (1) is composed chiefly of communis fibers, and that it corresponds to the communis element of the r. maxillaris of *Menidia*.

The r. mandibularis trigemini. Just after the infra-orbital trunk has emerged from the cranium and as it is dividing into its component rami, the r. mandibularis V gives off a large motor nerve which turns both cephalad and caudad in the m. adductor mandibulæ to supply its several muscular slips. This consumes most, but not all, of the motor fibers of the r. mandibularis V.

Together with the last large sensory (general cutaneous) twig is given off from the r. mandibularis V, which runs cephalad directly under the eye ball and over the m. adductor mandibulæ and laterally of the parent nerve. This twig is followed at once by two other smaller ones, one sensory and one motor. And a little farther cephalad, under the caudal part of the eye-ball, most of the remainder of the motor fibers separate. The two motor twigs enter the cephalic part of the m. adductor mandibulæ and need concern us no further. The two sensory twigs give off minute branches which supply the skin under the eye.

Under about the middle of the orbit, i. e., at about the level at which the n. opticus enters the eye ball, the r. mandibularis V turns outward and downward away from the maxillary and buccal rami between slips of the m. adductor mandibulæ,

to enter the lower jaw. In this region we find scattered through the more deeply staining general cutaneous fibers strands of very fine and more feebly staining nerves. These I take to be the communis fibers.

Having reached the mandible, a large branch is given off ventrad, which divides into two parts, an inner and an outer. The latter runs down external to the bones of the mandible to supply the overlying skin. The inner part runs down internal to all of the bones of the mandible and to the r. mandibularis externus VII, sends a twig caudad and another one cephalad along the dorsal border of that nerve and then enters the mandibular lateral line canal from its inner face through the same foramen as the lateralis twig for the sixth canal organ and supplies the skin of the ventral edge of the mandible in this region. The little twig of fine fibers which accompanies the r. mandibularis externus cephalad is joined still farther cephalad by motor fibers from the r. mandibularis V, as described below, and the mixed nerve thus formed runs into the isthmus to supply its skin and the m. genio-hyoideus. The twig which accompanies the r. mandibularis caudad is exceedingly minute. It runs back to the articulation of the mandible with the quadrate and then turns inward to supply the mucosa covering the articular and quadrate bones internally.

This twig is so closely applied to the r. mandibularis externus VII that the dissector relying upon gross methods only would almost infallibly consider that it takes its origin from this nerve. Nevertheless it preserves its individuality perfectly in the sections. No fibers could be traced from the r. mandibularis VII to the mucous lining of the mandible, though this nerve runs for a long distance in the earlier part of its course in the mandible immediately under this mucosa and careful search was made for such fibers. It is probable that the whole mucous lining of the hyoid and suspensory structures is innervated from the trigeminus.

The r. mandibularis V now runs forward along the outer face of the mandible parallel with the dorsal edge of the articular bone, and later along the inner face of the latter between

it and the *m. adductor mandibulæ*. Here another little coarse fibered twig is given off for this muscle, and a little farther cephalad the *r. mandibularis V* divides into two branches, a dorsal and a ventral. The dorsal branch retains the original position; the ventral one runs down external to Meckel's cartilage, between it and its investment of membrane bones, then turns inward around the ventral side of the cartilage to join the *r. mandibularis externus VII*, which at this level runs along the inner side of Meckel's cartilage. This ventral branch includes all of the remaining coarse fibers of the *r. mandibularis V*. These motor fibers with a few fine (sensory) ones now run up between Meckel's cartilage and the *r. mandibularis VII* to join the small bundle of fine fibers which runs along the dorsal side of the *mandibularis VII* and which has already been described as coming from the *mandibularis V* in the earlier anastomosis. The mixed motor and general cutaneous nerve thus formed runs for some distance cephalad along the dorsal surface of the *r. mandibularis VII*, then turns inward into the isthmus. The sensory fibers innervate the skin of this region, the motor fibers the *mm. genio-hyoideus* and *intermandibularis*, anastomosing behind with the *r. hyoideus VII*. The remainder of the ventral branch meanwhile has wedged in between Meckel's cartilage and the *r. mandibularis externus VII*, the cartilage being external and the *mandibularis externus* internal to it. The two nerves do not mix. The trigeminal nerve gives off numerous branchlets from this point cephalad for the skin of the mandible.

The dorsal branch of the *r. mandibularis V* continues to run forward internal to the outer lamella of the dentary bone, and farther toward the tip of the mandible running farther ventrally so as to lie dorsal to Meckel's cartilage, crossing over it to lie close to the *r. mandibularis externus VII*. We have, then, in the alveolar canal near the tip of the mandible the Meckel's cartilage lying adjacent to the outer lamella of the dentary bone and a wide space mesially of the cartilage containing the ventral branch of the *r. mandibularis V* in its ventral part, the *r. mandibularis externus* in its central part, laterally

and dorsally of the first mentioned nerve, and finally the dorsal branch of the r. mandibularis V, dorsally and laterally of the r. mandibularis externus VII. The nerves do not mingle, though they lie adjacent.

The dorsal branch at the tip of the mandible distributes one twig in the alveolar canal of the dentary bone; the remainder spreads out under the skin of the lower lip. These fibers unquestionably distribute mainly to the terminal buds with which the lower lip, like the upper, is abundantly supplied.

The ventral branch sends twigs down to the skin of the tip of the mandible, these accompanying the branches from the r. mandibularis externus VII through the dentary bone into the canal and thence ventrad to the skin. At the level of the first mandibular canal organ all of the remainder of this ventral branch turns inward and slightly backward to enter the mental barblet.

The structure of this barblet, though but imperfectly shown in my preparations, is very interesting. The epidermal covering is a very thick epithelium, consisting in places almost wholly of large terminal buds crowded close together. Beneath this is a thin, but dense, chorium, then a wide space between this and the thin supporting rod filled, completely with nerve fibers from the mandibularis V nerves of the two sides of the head.

A large proportion of these fibers are unquestionably communis nerves. It is probable that not all are such and that the barblet has an extensive general cutaneous innervation as well, since among the very fine nerve fibers are a few scattered ones of large size—a condition characteristic of general cutaneous nerves and one to have been expected on *a priori* grounds.

We have, then, traced communis nerves into the r. mandibularis V at its proximal end and traced this nerve distally into structures known to be typically innervated by the communis system. The course of these communis fibers can therefore be safely inferred, even though we have not been able to distinguish them from the accompanying general cutaneous nerves for their entire course.

That none of the terminal buds on the lower lip are supplied from the r. mandibularis VII (as occurs in *Menidia*) I think is certain, for that nerve in *Gadus* carries no appreciable number of fine fibers into the mandible, nor can any of its fibers be traced into regions where these buds abound.

9. *The Ramus Palatinus.*

The origin of the r. palatinus from the geniculate ganglion has already been described. Upon emerging from the cranial cavity through the common trigemino-facial foramen it curves around the ventral side of the VI nerve (Figs. 8, 9) and passes over the m. adductor arcus palatini and under the m. rectus externus toward the median line. It continues cephalad close to the parasphenoid bone and above the m. adductor arcus palatini for a long distance, far cephalad of the brain, before it passes down through the muscle to lie in its customary position adjacent to the mucosa of the roof the mouth. This mucosa carries taste buds both in front of and behind this point. Fibers appear to work their way down through the muscle to the subjacent mucosa and there spread out for the taste buds. This course of the nerve through the muscle is doubtless the explanation for the statement of Stannius ('49, p. 56) that the branches of the r. palatinus supply the m. adductor arcus palatini.

Other communis fibers arise from the ventral end of the geniculate ganglion along with the r. palatinus, as described in connection with the communis roots. This large bundle of fibers lies just within the trigemino-facial foramen and the first sympathetic ganglion lies just external to it, both internally of the other emerging roots of the trigemino-facial complex (Fig. 6). This level lies some distance cephalad of the ventral part of the geniculate ganglion from which these communis fibers arise and, though the sympathetic ganglion here rises up and lies in contact with these facial fibers, there is no opportunity for confusion of its cells with those of the geniculate ganglion.

There is an interchange of non-medullated fibers between

the intra-cranial fiber complex and the extra-cranial ganglion, the nature of which it is impossible to make out in Weigert preparations. But in addition to this, in the figure it will be seen that a small compact bundle of communis fibers separates from the others and passes into the sympathetic ganglion (*Jac. anast. + r. pt. VII.*). These fibers pass through the sympathetic ganglion caudad, and before the caudal end of the ganglion is reached withdraw from it, turning ventrally. These communis fibers take two courses. The first part continues directly caudad and constitutes the Jacobson's anastomosis of Cole. The other fibers run down along the inner face of the m. adductor hyomandibularis, spreading out under that muscle upon the mucosa of the roof of the mouth, which is here richly supplied with glands and taste buds.

10. *The Ramus Pre-trematicus Facialis.*

These fibers last mentioned correspond in their distribution exactly to what I have termed the r. pre-trematicus VII in *Menidia*. Several twigs turn cephalad upon the mucosa near the median line. The larger part spreads out over the cephalic face of the pseudobranch, some fibers penetrating that organ, others supplying the sub-jacent mucosa.

11. *Jacobson's Anastomosis.*

These fibers, like the last, are of fine caliber and are obviously communis fibers. From the first sympathetic ganglion they run directly back, as already indicated, close to the cranium. The sympathetic commissure between the facial to the glossopharyngeal nerves runs back from the extreme caudal end of the first sympathetic ganglion, independently of the fibers of Jacobson's anastomosis and dorsally of them. The sympathetic fibers are mainly non-medullated, while those of Jacobson's anastomosis take the Weigert stain vividly. A little farther back these two fiber bundles run close together accompanying a big blood vessel, the Jacobson's anastomosis dorsally, but they do not fuse. The Jacobson's anastomosis runs into the cephalic end of the IX ganglion; the sympathetic commissure runs along the inner face of this ganglion closely applied

to it, yet distinguishable, leaving the ganglion caudad to join the sympathetic chain on the vagus. In this I confirm the anatomical findings and morphological interpretation of Cole.

12. *The Ramus Lateralis Accessorius.*

The r. recurrens facialis, or facial root of the r. lateralis accessorius, arises from the geniculate ganglion by three rootlets, which will be designated as the first, second and third rootlets, counting from behind cephalad.

The first one is the largest and can be regarded as the main root. It will first be described. From the extreme ventral tip of the geniculate ganglion (which lies internal to and ventrally of the ventral lateral line root) a large bundle of communis fibers (Figs. 1 and 4, *rec. 1*) arises and curves around the lower and outer side of the ventral lateralis root, running directly dorsad along the outer face of the V + VII root complex and along the inner side of the membranous ear. The fibers arise mainly from cells in the extreme ventral tip of the geniculate ganglion, but partly higher up from the cells of the ganglion which border the inner face of the ventral lateral line root. They are of exceeding fine caliber and delicate myelination, thus appearing paler than the other fibers of the complex.

A smaller bundle of nerves arises from the ventral tip of the geniculate ganglion a little farther cephalad than the first rootlet. This is the second rootlet. Its course is similar to that of the first (Figs. 1 and 5, *rec. 2*). It runs cephalad a short distance from the tip of the geniculate ganglion along the ventral surface of the ventral lateralis root. The latter runs cephalad to its foramen, then, while in the foramen, turns sharply back to enter the truncus hyomandibularis. In the caudal, or concave, surface of this curvature this second rootlet turns abruptly dorsad just inside the hyomandibular foramen, and crosses the outer surface of the intra-cranial portion of the lateralis root just mentioned to lie in the angle between the dorsal and ventral lateralis roots. Here it is joined by the third rootlet and these two rootlets then run up to join the first rootlet.

At about the same transverse plane as the origin of the first rootlet a portion of the geniculate ganglion, as already mentioned, is wedged in between the trigeminal root and the ventral lateralis root, lying internally to these roots. The third rootlet arises from the geniculate ganglion at this point (Figs. 1 and 5, *rec. 3.*). Its fibers, however, do not rise wholly or chiefly from these cells, but from cells of the geniculate ganglion lying farther mesially, viz. those in the most dorsal and cephalic portion of the ganglion, and from its middle portion farther caudad. As the fibers squeeze through between the trigeminus and ventral lateral roots, they turn caudad, bordering the most caudal edge of the Gasserian ganglion, which runs back in the same notch between the trigeminus and ventral lateral roots but on the outer side of the roots. There is no evidence that the lateralis accessorius rootlet receives any fibers from the Gasserian ganglion; in fact the appearances are all against such a connection, though some points in the peripheral distribution would suggest it. In any case the number of such fibers would be very small, both absolutely and as compared with the number of communis fibers from the geniculate ganglion. The third rootlet, as stated above, is joined by the second rootlet and the two run back in the same position to join the first root.

As already indicated, the three rootlets from the geniculate ganglion having fused to form the r. recurrens VII run directly dorsad. As it passes along the outer side of the dorsal lateralis root, it receives from the most extreme dorsal edge of the lateral line ganglion a very few coarse fibers (Fig. 3, *l. rec. VII.*), which may be followed from this point on among the fine communis fibers.

The root, as thus composed, continues directly dorsad in the meninges along the lateral aspect of the optic lobe and passes through a foramen in the top of the cranium.

Just before its emergence from the cranium it receives an addition from behind. This is the vagal root of the r. lateralis accessorius, which is much smaller than the facial root and like it contains a few coarse fibers along with the very fine ones. This root in my specimens agrees, with some variation in de-

tails, with Cole's description. Arising in two rootlets from the first (most cephalic) root from the lobus vagi (sensory IX + first sensory vagus root), it runs internal to the roots of the r. lateralis vagi and the VIII nerve, then near the apparent origin of the former nerve divides, one moiety running dorsad, internal to the r. lateralis X, the other external to it. On each of these portions there is a ganglion, the two ganglia being distinct and on opposite sides of the lateral line root. The nerves arising from these ganglia merge dorsally of the lateral line root and continue dorsad and cephalad as the vagal root of the r. lateralis accessorius, running up along the outer face of the cerebellum intra-cranially to join the facial root, as already described.

The vagal root of the r. lateralis accessorius clearly arises mainly from the common IX + X root, as just described, i. e., is composed of communis fibers. It runs out, however, so close to the intra-cranial jugular ganglion that it is impossible to be sure that it does not carry out with it some general cutaneous fibers from this source. This may account for the scattered medium sized fibers observed in this root, though I think it more probable that these come from the r. lateralis vagi, with which this accessory lateralis root is still more intimately united. In this case these fibers, like the similar lateralis fibers found in the facial root, doubtless distribute to pit-organs of the top of the head.

Upon emergence from the cranium, the r. lateralis accessorius turns directly caudad, gradually becoming separated from the cranium by the dorsal musculature. Having reached the region of the supra-temporal canal, this nerve lies close under the canal at its dorsal end. It has meanwhile given off a number of small branches, composed chiefly of fine fibers, but with some of medium size. Some of these run cephalad from the foramen, some caudad. Their minute ramifications spread out under the skin. None of these branches could be traced to specialized sense organs, though this negative evidence is of little value, as the skin here is not well preserved in my specimens.

Those branches of the r. lateralis accessorius which run back under the skin in the neighborhood of the supra-temporal canal enter a cutaneous area which also receives numerous very delicate nerves from the vagus. These latter are partly general cutaneous and partly lateralis fibers from the r. supra-temporalis vagi for pit-organs. The twigs from the r. lateralis accessorius effect minute terminal anastomoses under the skin with both kinds of vagal twigs, so that the innervation of this whole region is exceeding difficult to analyze.

I find a row of large pit-organs just in front of the supra-temporal canal and approximately parallel with it, which evidently corresponds to the organs figured by Cole in the same position. They are innervated by coarse fibers from the r. supra-temporalis vagi (Fig. 1, *st. X*). I have also found the row of four or five pit-organs figured by Cole on his figure I, running from the region of the supra-temporal canal back near the median line to the beginning to the dorsal fin. They are all supplied by nerves arising from the dorsal branch of the r. lateralis vagi, leaving that nerve in connection with the twig for the sixth organ of the lateral line of the trunk (Cole's nomenclature). This nerve is evidently the one marked L⁶ on Cole's Fig. 2. It runs up and crosses the lateralis accessorius, running internal to its ventral branch and external to its middle branch and very closely joined to them.

In the region of the supra-temporal canal the r. lateralis accessorius divides into three branches. The dorsal one is destined for the base of the dorsal fin, the middle one for the base of the anal fin and the ventral one for the paired fins. The dorsal one sends first several small twigs up under the skin toward the median line and then breaks up into an open plexus which passes up and joins the branches already given off. The larger of these branches are gathered near the mid-dorsal line in the inter-muscular septum between the interspinal and the general dorsal muscles. This nerve is therefore formed very much as in *Menidia*, though the plexus formation at its origin is extra-cranial instead of intra-cranial. The anastomosis with

the dorsal rami of the successive spinal nerves occurs in the typical way.

In the region of the pectoral girdle where the dorsal branch of the r. lateralis vagi becomes superficial the accessory lateral line nerves cross the lateralis vagi. In regard to the relations of these nerves, I confirm the figure of Stannius ('49, Plate III, Fig. 2). The middle and ventral branches of the accessory nerve embrace the dorsal lateral line nerve without anastomosing with it, one going external, the other internal. The branch for the anal fin takes the internal course, but some of these fibers separate from this nerve and later join the branch for the paired fins. All of the accessory lateralis fibers anastomose more or less in this region with medial rami of the spinal nerves. The nerve for the anal fin crosses the ventral branch of the r. lateralis vagi externally. It was not traced to its termination.

The nerve for the pectoral fin is small. It joins the brachial plexus and its fibers could not be separately followed into the fin.

The nerve for the pelvic fin is much larger. It enters that fin in two branches in connection with spinal nerves, one branch at the cephalic and one at the caudal end of the attachment of the fin. The accessory lateralis fibers could not be followed separately from the spinal nerves.

The pelvic fin is sparsely covered at the angles, particularly the outer edge, with very minute terminal buds. These do not at all resemble the "pit-organs" of the head, as I have found them in these same specimens. The latter are broad and flat topped. They are not in fish of this age sunken into pits, but exposed upon the skin and slightly projecting above it, just as in the adult of *Menidia*. They extend down through the epidermis to rest upon the dermis, which is often thinner under them and raised up into a ring-shaped elevation projecting up into the epidermis around the border of the organ. This area of dermis is perforated in its center for the nerve. The nerve fibers are of medium size and very densely myelinated, so that they stain intensely.

These terminal buds of the fins, on the other hand, are

much smaller and they rest in a layer of thicker epidermis, through the whole thickness of which they do not extend, so that they do not reach the dermis. The nerve fibers are exceedingly fine and in my specimens are so thoroughly decolorized that it is usually impossible to see them at all. When they appear it is only as delicate colorless filaments running from the base of the organ to the dermis. The organs are never flat topped, but always pointed at the apex and project very slightly above the general surface of the skin. They differ from the terminal buds of the cyprinoids and siluroids in that there is no dermal papilla rising up through the lower layers of the epidermis for them to rest upon, and they are broader, nearly globular with a pointed apex, instead of narrowly flask-shaped. A few scattered terminal buds were found on the pectoral fin similar to those on the pelvic.

My sections do not afford an absolute demonstration that the communis fibers which enter the paired fins supply the terminal buds there found. Nevertheless the fact that terminal buds are not found on these fins in such fishes as *Menidia*, which do not have the corresponding communis nerves, together with the known correlation of terminal buds and communis nerves in every other case of which we have accurate knowledge, give such an assumption the highest degree of probability.

The sections unfortunately do not extend far enough caudad to enable me to study the dorsal and anal fins. Yet I have no doubt that the distribution of their communis nerves is strictly analogous to that of those just considered.

13. *The Pre-vagal Sympathetic System.*

The sympathetic system in its cephalic part is much more highly specialized in *Gadus* than in *Menidia*; nevertheless its relations to the trigemino-facial complex are clear in their main outlines. Since it lies almost wholly internal to the other nerves of the complex, it is impracticable to sketch it upon the reconstruction. The series of transections will, however, illustrate its course.

The sympathetic ganglia of the trigemino-facial region corresponding to the first, second and third ganglia of *Menidia* and some other fishes are here fused into a single elongated ganglionated strand, which follows the course of the orbital vein. This wide vein or sinus, runs along the inner side of most of the trigemino-facial complex between the third nerve above and the sixth nerve below.

The sympathetic chain runs from the IX + X root complex extra-cranially parallel with Jacobson's anastomosis, though without fusing with it, to the V + VII root complex, as already described (Figs. 2, 3, 4, *sy.*). Just behind the trigemino-facial foramen it expands into a large ganglion (Fig. 5, *sy.*) This ganglion runs up into the foramen (Figs. 6 and 7, *sy. g.*) and in the narrow space under the emerging ventral lateralis root is crowded in with the orbital vein, the motor VII and the communis fibers for the r. pre-trematicus VII and Jacobson's anastomosis. These nerves are all very intimately mingled. The communis fibers last mentioned pass out directly through the middle of the sympathetic ganglion, though the Weigert sections leave no doubt that these fibers do not arise in the sympathetic ganglion. The motor fibers for the m. adductor arcus palatini pass out close to these, curving around the dorsal and outer side of the ganglion.

Having passed inside of the foramen, the sympathetic ganglion becomes reduced to a narrow strand of cells with many fibers. This strand passes around the outer side of the blood sinus from its ventral to its dorsal side (Fig. 8, *sy.*) internal to the emerging infra-orbital trunk. It then turns cephalad (from this point on non-ganglionated) along the dorsal side of the blood vessel and under the forward extension of the Gasserian ganglion for the r. ophthalmicus superficialis V. As we pass cephalad, this blood vessel divides into two and the sympathetic nerve runs between its two divisions and joins itself to the dorsal surface of the III nerve (Fig. 9, *sy.*) Its further course has been partially worked out. It follows the still undivided III nerve forward and after that nerve has given off its branch for the m. rectus superior the sympathetic accompanies the

main nerve. After a short course a large ciliary ganglion is formed, which is closely applied to the III nerve, so that it is not possible to distinguish the long and short roots of the ciliary ganglion.

Just cephalad of the ciliary ganglion the III nerve divides into three branches, one of which continues forward in about the original relations and in the middle of the orbit supplies the m. rectus internus. The other two turn ventrad. One passes around the outer side of the m. rectus inferior to continue cephalad along its ventral border and closely external to the r. palatinus to supply the m. obliquus inferior. The other continues along the dorsal border of the m. rectus inferior and innervates it.

The sympathetic ramus ciliaris brevis after separating from the ciliary ganglion accompanies for a short distance the III nerve for the m. rectus internus, then separates from this and joins itself to the dorsal surface of the orbital vein, finally to follow the ventral face of the optic nerve, with which it enters the eye ball.

I may add in passing that a diagram of the relations of the eye-muscle nerves based on Allis' scheme ('97, Plate XXII, Fig. 12) shows no important differences from the one which I constructed for *Menidia* ('99, Fig. 13), save in the absence of the vestigial r. ophthalmicus profundus.

14. *The N. Glossopharyngeus.*

Stannius' description of the IX roots of *Gadus* is confirmed. The IX root of Cole (p. 176) is the first root of Stannius. It arises far forward and ventrally, under the origin of the r. lateralis vagi. This is the motor root. It runs up and back close to the brain between it and the posterior VIII root, then becomes wedged in between this and the root of the r. lateralis vagi (these two acustico-lateralis roots being here closely united), and then continues back along the ventral face of the r. lateralis vagi until the first root from the lobus vagi emerges from the brain.

Cole describes (p. 176) fibers from this IX root to the

vagal root of the r. *lateralis accessorius*. I do not find them. The two nerves lie close together, but since this IX root is motor, a connection with the r. *lateralis accessorius* would of course be quite inexplicable.

The first sensory root of the vagus complex is quite large and is a mixed glossopharyngeus and vagus root. It runs out under the r. *lateralis vagi*, the motor IX and the VIII roots, becoming ganglionated at once. This intra-cranial ganglion is, however, a small one and cannot pertain to more than a very small proportion of the fibers of this root. It cannot be the IX ganglion, as that is extra-cranial and the IX fibers can be seen to run directly through this ganglion. It is, in fact, the jugular, or general cutaneous ganglion of the vagus.

From this first sensory root, fibers separate to join the motor IX root and the mixed root thus formed runs out laterally and forwards to its extra-cranial ganglion in the usual way. From the ganglion the first truncus branchialis turns backward and outward, while the sensory bundle which accompanies the sympathetic chain to form Jacobson's anastomosis separates from the cephalic end of the ganglion.

The first nerve to be given off from the truncus is the motor twig for the first internal levator arcus branchii. A little farther out, the motor nerve for the first external levator arcus branchii is given off. The arrangement of the branchial rami of the IX and X nerves is in general as in *Menidia*. The post-trematic ramus divides into two branches, inner and outer, one following the concave, the other the convex surface of the branchial bar, while the minute pre-trematic ramus of the next following branchial nerve follows the convex surface parallel and close to the much larger outer post-trematic of the same gill. The outer post-trematic ramus lies at the base of one demibranch, the pre-trematic over the other in each gill. In *Gadus*, as in *Menidia*, the post-trematic nerve is evidently mixed, the sensory fibers far out-numbering the motor.

The pre-trematic IX nerve is exceedingly tenuous and I found it impossible to trace it to the pseudobranch, though Stannius states that the pseudobranch is innervated from the

IX nerve in *Gadus* ('49, p. 77). If glossopharyngeal fibers reach the pseudobranch at all, they must play a very subordinate rôle in the innervation of that structure, as compared with the facialis fibers, which I have found spread out over its whole anterior surface. The innervation here, as in *Menidia*, speaks loudly in favor of regarding the pseudobranch as belonging distinctively to the facial segment.

15. *The Cutaneous Root of the Vagus.*

Only a few points in the morphology of the vagus will be touched upon. The relations of the general cutaneous component of the vagus are the chief points of interest in this connection. The communis roots of the vagus and glossopharyngeus are long, as their ganglia lie wholly extra-cranially, as usual among the teleosts, and the cranial wall is here much farther from the brain than in *Menidia*. The vagal roots arise much as in *Menidia*, the lateralis root running out dorsally of all of the others and the motor roots ventrally. The general cutaneous component is larger than in *Menidia* and arises from the spinal V tract in the caudal region of the root complex and going out with its first root. Its ganglion, the jugular ganglion, is intra-cranial and lies as close as possible to the brain, for the most part ventrally of the other root fibers. It is therefore far separated from the other ganglia of the vagus.

The fibers arising from the jugular ganglion run out and up along the cephalic side of the root complex and pass out of the cranium appressed to the ventral side of the lateralis root. They pass into the r. supra-temporalis vagi, and accompany these lateralis fibers to the skin about the lateral line canal near the supra-temporal commissure. Thus the r. cutaneous dorsalis and the r. supra-temporalis are in *Gadus* fused into a common trunk. This is clearly the course of most of the fibers from the jugular ganglion. There may be other fibers, though I was unable to trace any others through the complex.

The vagal root of the r. lateralis accessorius arises from root fibers which pass very near to the jugular ganglion, but I could not demonstrate any fibers from this ganglion to that

root, which has, moreover, its own ganglia farther cephalad.

16. *The Trapezius Muscle.*

In view of the discovery of a true trapezius muscle in *Menidia* ('99, Section 5, IX), innervated from the vagus, I have examined the corresponding region in *Gadus*. Here I confirm the conclusion of Vetter ('78, pp. 526 and 541) that a true trapezius muscle is absent. The muscle running from the cranium to the pectoral girdle in *Gadus* is innervated from the spinals and not from the vagus. It therefore is merely a detached portion of the general dorsal musculature.

17. *The Nerves for the Pharyngo-clavicularis Muscles.*

In the case of these muscles too my findings in *Menidia* were at variance with those of some other observations, and I have examined the condition in *Gadus*. The internal and external pharyngo-claviculares are arranged essentially as in *Menidia* and the innervation is also the same. That is, these two muscles in *Gadus* are supplied by nerves arising from the œsophageal rami of the vagus. The r. cervicalis of the first spinal nerve runs along the inner side of both of them, but does not participate in their innervation. The morphological significance of this feature of the nervous system of the teleosts has been touched upon in my previous contribution ('99, Section 5, VII, 5, v).

III. COMPARATIVE PART.

The reader who will compare the nerves of *Gadus* as worked out by Cole (for the lateral line system) and myself (for the other systems) with my findings in the nervous system of *Menidia* cannot fail to be struck with the very close similarity. In fact the differences of real morphological importance are very few indeed. Chief of these is the absence in *Gadus* of a communis component in the truncus hyomandibularis i. e. the r. mandibularis internus VII, and in correlation with this the presence of such fibers in the r. mandibularis V.

The explanation of this condition is not easy. It is, however, probably to be sought in the presence in *Gadus* and not

in *Menidia* of a mental barblet bearing terminal buds. The presence of this barblet and its nerve in *Gadus* also cooperates with the larger size of the r. recurrens VII to account for the larger fasciculus communis as compared with that of *Menidia*.

Another difference of importance is in the arrangement of the roots of the r. lateralis accessorius. In both cases this nerve is composed wholly or nearly so in its cranial portion of communis fibers derived chiefly from the geniculate ganglion, but partially from post-otic communis roots. The smaller root in *Menidia* I think comes from the IX; in *Gadus* it comes from a mixed IX + X root. The post-auditory root joins the pre-auditory intra-cranially in *Gadus* and extra-cranially in *Menidia*. Some reflections upon these connections have been offered in my previous contribution ('99, Sec. 12).

Again, the pre-auditory sympathetic is in a much more highly differentiated condition in *Gadus* than in *Menidia*, the first three ganglia having fused into one, which is chiefly extra-cranial and associated most closely with the roots of the facial nerve. The ciliary ganglion appears to have but one root and in other respects the sympathetic nerves of the orbital region are highly specialized.

The absence of the trapezius muscle with the corresponding motor branch of the vagus in *Gadus* is another noteworthy difference which is difficult of explanation.

Most of the other differences are correlated with the more elaborate development in *Gadus* of the specialized cutaneous sense organs, viz., the lateral line organs (including the pit-lines) and the terminal buds. The so-called pit-organs, it should be noted, in the young cod fish which I have examined microscopically are not contained in pits, but, as in the adult *Menidia*, are strictly naked sensory papillæ, usually projecting slightly above the surrounding skin. A brief comparison between them and the terminal buds is given near the close of Section 12 in the preceding part of this article.

The discrepancies between Cole's results and my own, to which reference has already been made, refer almost wholly to the relations of the geniculate ganglion and its related structures,

particularly the pre-vagal sympathetic and the r. lateralis accessorius. Let us take up the analysis of the trigemino-facial complex as given on p. 133 of his paper.

(1) His lateral line ganglion requires no further comment. My findings agree with his description.

(2) His "trigeminal or Gasserian" ganglion "is situated internal and largely anterior to the second or ventral portion of (1). From this portion of the complex the superficial ophthalmic of the trigeminus, the maxillo-mandibular trunk, and, probably, the post-branchial division of the facial arise. If the latter statement be correct, as seems certain, this ganglion should be called the 'trigemino-facial.'" The last supposition proves to be correct. We have two quite distinct ganglia here, the Gasserian and the geniculate or facial, as my descriptions in the preceding part have shown. If these two ganglia are clearly distinguished (which Cole failed to do) the difficulty, to which the author refers in the foot-note, in the interpretation of the morphology of the proper Gasserian ganglion of *Gadus*, does not exist. The case is perfectly simple; the Gasserian ganglion is strictly homologous with the ganglion of that name in *Menidia*, *Rana*, *Amblystoma* and all other vertebrates in which it has been clearly distinguished from the other ganglia of the complex. From the fishes to man this ganglion gives rise to all of the pre-auditory general cutaneous fibers and, so far as now known, to no others.

(3) His "facial" ganglion is thus described: "This is a long and perfectly distinct ganglion which lies ventral to (2). It is connected with the palatine nerves and also with the pre-spiracular or chorda tympani divisions of the facial. It also communicates (a) directly with the sympathetic trunk; (b) by means of Jacobson's anastomosis (see below) with the glosso-pharyngeus." This description was most puzzling to me until I discovered that the "facial" ganglion here referred to is in reality the sympathetic ganglion. The more detailed account of this ganglion which he gives on p. 135 leaves no doubt of this.

How, then, shall we account for the fact that the "facial

proper" of Cole, viz., the palatine, 'pre-spiracular VII, Jacobson's anastomosis, etc., arise from this extra-cranial sympathetic ganglion? Cole's explanation is that his "facial" ganglion represents a portion of the trigemino-facial complex which is "in the act of migrating from its original position and becoming converted into a typical sympathetic ganglion." The fact is, however, that none of the nerves mentioned above, except the sympathetic trunk, have any real connection with this ganglion, but, as we have seen, they pass either through or around it to enter the true facial, or geniculate ganglion intra-cranially. They appear to arise from it merely because of the way the sympathetic ganglion is crowded up into the foramen among these roots.

A glance at my figures 6 and 7 and the accompanying description will show how easily such a mistake could arise, especially if the sections were not exceptionally well preserved and differentially stained. It would be a matter of the most extreme difficulty to analyze this complex with other than the best Weigert sections; nevertheless, given such preparations, I think that the facts can be ascertained with precision. In *Gadus*, then, as in *Menidia*, I find the sympathetic and geniculate ganglia both present and clearly separate.

Cf. paragraph 3) of Cole's "Notes," immediately following this article. Without desiring to continue this controversy, I feel that a word of further explanation is necessary in this connection. I freely admit that my preparations do not demonstrate that *no fibers* from the sympathetic ganglion enter the communis nerves in question. In fact there is every reason to suppose that some such sympathetic fibers do go out with these nerves. A sympathetic ganglion in *Menidia* (and most other teleosts) is typically placed on the root of each of the cranial nerves of the branchial type and in several of these I have seen large bundles of fibers leave these sympathetic ganglia and enter the peripheral nerves on whose roots they are placed. Compare Fig. 3, *sy. 1*, *sy. 2*, *sy. 3*, of the *Menidia* paper.

I am, however, convinced that such fibers, if present, are true sympathetic, and not facial fibers, for two reasons: (1) by analogy with other vertebrates where the geniculate and the sympathetic ganglia are more clearly separable and where these nerves have always been described as arising from the facialis; (2) because in *Gadus* the undoubted facial root is of sufficient size to form these nerves without the aid of hypothetical "facial" fibers from the sympathetic ganglion.

Finally, I think that there *are* mechanical necessities, at least in fish of the age which I have examined, which explain fully the anomalous position of this sympathetic ganglion in *Gadus*. The infra-orbital and hyomandibular trunks pass out through a single foramen, in which all of the contained structures are very much crowded (cf. Fig. 6). The sympathetic chain enters the cranium through the same foramen, and since this is the sympathetic root ganglion for both the VII and the V nerves it lies partly within and partly without the foramen. This being understood, its intimate relation with the emerging communis branches of the facialis (which also, as in *Menidia*, pass out in the same space between the hyomandibular and infra-orbital trunks) follows of necessity.

Now, when it comes to the identification of the branches which Cole describes on p. 135 as arising from his "facial" ganglion, I have experienced greater difficulty, nor am I certain that the comparisons which follow are free from error.

His ventral part of the hyomandibular trunk, or "facial proper" evidently corresponds to the communis fibers which I have described and figured as arising from the cephalo-ventral angle of the geniculate ganglion. Cole says, "The first branch to be given off from these fibers passes through the inner region of the facial ganglion, turning inwards, downwards and forwards, and passing among the muscles of the alimentary canal." The second branch "passes almost through the middle of the ganglion and courses forwards external to the previous branch." "The third and largest branch passes obliquely through the center of the ganglion, turns inwards, and then divides to form two large nerves—one of which passes forwards and the other backwards. The forward division again divides, and represents the true palatine branch of the facial nerve and its two divisions, the anterior and posterior palatine nerves described by Allis in *Amia*. The posterior division passes backwards and slightly outwards and accompanies the cephalic sympathetic trunk, but has otherwise no connection with it." The last is Jacobson's anastomosis. The identification of it and of the true palatine and posterior palatine offer no difficulties here, the posterior palatine being the nerve which I have called the r. pre-trematicus VII. But I have not been able to satisfy myself regarding the identity of the first and second branches of Cole's description. They may be the nerves for the m. adductor hyo-

mandibularis and adductor arcus palatini, or either or both the first and second branches may be detached branches of the r. pre-trematicus VII. My Fig. 5 shows how this nerve breaks up and spreads out between the pseudobranch and the m. adductor arcus palatini.

Cole goes on to say, "The remainder of the ventral fibers of the hyomandibular pass outwards with the latter trunk and the facial ganglion, but apparently have no connection with it, and are continued as the pre-spiracular or chorda tympani division of the facial." This is another nerve which I cannot identify with certainty. In the first place, the language used is not clear. Is the antecedent of *it* "trunk" or "ganglion?" If the former, then this nerve might be the communis fibers which enter the r. mandibularis V. The context, however, does not favor this. If *it* refer to "ganglion," then it is probable that the author has reference to a communis component entering the truncus hyomandibularis, to form a r. mandibularis internus VII (in the sense in which I have used this term, not in Cole's sense).

Cole has stated in two other places in this paper (pp. 162 and 202) and also to me in private correspondence that he has found such a nerve in *Gadus*, adding that it "exactly corresponds to the 'internal mandibular' of Allis in *Amia*." I have failed to find any such nerve and am convinced that it does not exist in my specimens, nor can I be sure from his figures and descriptions what nerve he has in mind. Since Cole describes that nerve as "the pre-spiracular or chorda tympani division of the facial," it follows that I am not able to determine just what he means by that term, though from the fact that he describes it (p. 202) as arising from the base of the palatine and "forming a part of the same bundle of fibers," I infer that he has reference to a part of what I have termed the r. pre-trematicus VII. His nerve cannot include the whole of this ramus, since his "posterior palatine" must also be included here.

The problems connected with the chorda tympani I do not propose to re-open here. The extensive discussion in Sec. 7 of my *Menidia* paper was written with full knowledge of the

condition in *Gadus*, as here described, and I have now nothing to add to that argument.

Cole gives the origin of the post-branchial, or hyoidean branch of the facial "as doubtful from the 'trigeminal' ganglion." This I have confirmed so far as the sensory portion is concerned and can assert positively that these are general cutaneous fibers.

He follows with an exhaustive examination and criticism of the literature of the facial ganglion, in which he tries to show that the pre-spiracular ganglion of the elasmobranchs (which here is "still in very close association with the main facial ganglion") has in the more highly specialized teleosts become completely separate from the trigemino-facial complex, though still retaining many of the characteristics of a cerebro-spinal ganglion. "In short the facial ganglion of the cod is an exemplification of the principle of evolution, and shows us a stationary ganglion becoming converted into a vagrant or true sympathetic ganglion."

It is not necessary for us to review the details of this argument, for it is evident that its foundation has been totally destroyed by the discovery that Cole's "facial" ganglion is already a true sympathetic ganglion and as perfectly differentiated as such in *Gadus* as in any other vertebrate, and that it does not give rise to the palatine and other visceral sensory rami of the facialis. These on the other hand, arise from a totally distinct ganglion, the geniculate, which conforms in every way to a cerebro-spinal ganglion. There is no more evidence here than in any other vertebrate that the communis ganglion is becoming transformed into a sympathetic ganglion. The problem of the relation of the communis system to the sympathetic is a very important and a very difficult one, and Cole may be right that the sensory sympathetic is an off-shoot of this system; but before this conclusion can be accepted more evidence must be furnished.

Another important discrepancy in Cole's work is his failure to recognize that the r. lateralis accessorius takes its first, or pre-auditory, root-complex from the geniculate (facial) ganglion

and not from the Gasserian. Stannius, however, on p. 32 and elsewhere clearly states that the r. recurrens, the dorsal intracranial branches, etc., arise from the ganglion of his third root in connection with the r. palatinus and the other rami of this system. It is significant, however, that in the list of species of fishes exhibiting this arrangement which Stannius gives Gadus is absent, though we know that Stannius dissected several species of this genus. This is another illustration of the difficulty of separating the geniculate from the Gasserian ganglion in this type. They are, in fact, so similar and so close together that I doubt whether I should have been any more successful than Stannius and Cole if I had not had before me the case of Menidia, where error would be impossible.

Cole, moreover, does not deduce from the literature the same conclusions as my own in this connection. Thus, on p. 169, in discussing Baudelot's account he seems to confuse the anastomosis between the r. opercularis vagi and the r. opercularis facialis with the connection between the vagal and facial roots of the r. lateralis accessorius. There can be no doubt from the descriptions of Baudelot and others that the r. opercularis vagi (general cutaneous fibers) is in many cyprinoids intimately related to the vagal roots of the r. lateralis accessorius (communis fibers), but they must not be confounded. Compare the discussion of the rami cutanei dorsales vagi in my Menidia paper, section 5, VIII.

Again, in discussing (p. 174) the results of Haller ('96) he says, "Haller carefully redescribes the origin of Weber's accessorius (=accessory lateral in part) in *Cyprinus carpio*, where the accessorius is found in a very interesting, and perhaps primitive, condition. An anterior root (Taf. ii, figs. 7 and 8 a [it should be figs. 8 and 9]) is formed by the union of two twigs from the Gasserian ganglion, *one from each side*, and two twigs from the facial ganglion. This root passes backwards and anastomoses with the fused 'ventral roots of the vagus, (Gegenbaur), or what is usually identified as the Ichthyopsid 'hypoglossal.' From the ganglion of the latter close to the entry of the root above, arises one of the roots of the accessory lateral system, which

passes upwards, receives a root from the vagus, and then doubtless has the usual peripheral distribution."

Haller seems to regard this accessorius of the carp as a general cutaneous nerve contributing to the brachial plexus for the region of the pectoral fin. Cole regards it as a "somatic sensory," i. e., cutaneous, nerve from the Gasserian ganglion, which "collects" the dorsal branch of the "hypoglossal," and a vagal branch and then proceeds into the trunk to form the accessory lateral line nerve, there to collect the dorsal branches of the spinals. My own view of the accessorius of cyprinoids, as developed in Section 12 of the *Menidia* paper, is different from either. I have regarded it as an intra-cranial anastomosis between the geniculate ganglion and the vagal root of the r. accessorius. It should be noted that Haller's account is based on dissection only. He has made no accurate analysis of the trigemino-facial ganglia and there is no satisfactory evidence that the root in question arises from the trigeminal, or Gasserian ganglion, rather than from the facial, or geniculate ganglion. Haller does not state that the nerve arises in part from the facial ganglion, but from the "Facialisaste des Trigemini," and his trigeminus ganglion, judging from his figures, is quite as likely to be the geniculate.

Stannius' description ('49, p. 60) of the conditions of this root in the cyprinoids will prove, I think, much more accurate: "Was die Quelle des Ramus recurrens anbetrifft, so ist derselbe von der dritten Wurzel des Nervencomplexes, nämlich derjenigen, welche aus dem Lobus impar medullae oblongatae ihren Ursprung nimmt, abzuleiten. Diese starke Wurzel, welche ausschliesslich feine Primitivröhren enthält und motorischer Eigenschaften ermangelt, spaltet sich noch innerhalb der Schädelhöhle in mehre, schwer zu trennende und zu verfolgende Stränge. Einer derselben tritt über an den eigentlichen N. trigeminus und ist namentlich in den an der Austrittsstelle desselben gelegenen gangliösen Plexus zu erfolgen, gibt auch Elemente ab zu den in der Schädelhöhle aufsteigenden Nerven. Ein zweiter Strang hilft den N. facialis zusammensetzen. Ein drittes, beträchtlicheres Bündel tritt über in eine umfängliche

gangliöse Masse, welche längs der Austrittsstelle des N. facialis sich erstreckt und aus welcher ferner der in den Augenmuskelkanal absteigende starke N. palatinus hervorgeht, welche aber zuletzt der Ausgangspunkt des am Boden der Schedelhöhle nach hinten sich erstreckenden Ramus recurrens wird."

I quite agree with Cole that the internal courses and peripheral distribution of all of these fibers must be worked out in the cyprinoids before we can arrive at safe conclusions; but I have said thus much in order to meet another remark of Cole's. "It is hence perfectly clear that the accessory lateral nerves of fishes consist, as has been proved microscopically, of somatic sensory fibers." My examination of the literature has led me to no such conclusion, nor can I accept Cole's results as decisive in the matter.

But first of all, the matter of definition is important, for it appears from some correspondence which I have had with Mr. Cole that we use the term "somatic sensory" in slightly different senses. I have used it in the sense proposed by Strong, viz., as synonymous with "general cutaneous," or nerves distributed to the outer skin without specialized end-organs and terminating in the dorsal horns or their morphological equivalents in the head, viz., the spinal V tract and its associated nuclei. But Cole appears to use the term more nearly in Gaskell's sense, as applying to all cerebro-spinal nerves ending in the skin. He, however, excludes all lateral line nerves, but is not willing to exclude the communis nerves for terminal buds of the outer skin, though for what reason it does not appear, since these are quite as distinct from the general cutaneous nerves as are the lateral line nerves.

The fact that communis nerves from the geniculate ganglion do reach the outer skin can certainly no longer be doubted. If further proof of this were necessary, Kingsbury ('97) has shown that nature has performed a beautiful experiment, which may be said to settle the matter conclusively. For in cyprinoids and siluroids, where the accessory lateral nerves and their terminal buds are the most highly developed, they have been shown not only to belong to the facialis (certainly in the latter case

and probably in the former), but to have evoked in the medulla oblongata special terminal nuclei, the "lobus trigemini," or "tuberculum impar" of these fishes.

The problem of the relation between the cutaneous and the visceral fibers of the communis system I have touched upon in another place. I do not claim to have settled it. It may be "unphilosophical" to associate these diverse structures in a single system, but they *are* thus associated in our specimens and we have not thus far succeeded in dissociating them. In the present state of our knowledge it is better to stick to the facts, whether they accord with theory or not. But even from the theoretical standpoint it is difficult to account for the migration of general cutaneous fibers from the head into the trunk in any such numbers as we find them in siluroids and other forms with the accessory system well developed, for these regions have their own general cutaneous nerve supply from the spinals. From the account of Harrison's dissections of the gold fish ('95, p. 509), from the results of Allis ('97) and from my own study of the recurrent nerve of *Menidia*, as well as from the results presented in this paper, I am convinced that this nerve supplies the terminal buds of the body and not the general cutaneous areas.¹ This Cole seems to admit (p. 177); his error lies in associating these organs with the ordinary somatic sensory nerves. We have no evidence that they are ever supplied by the general cutaneous nerves.

As for the motive for the migration of the terminal bud system into the trunk, we can scarcely conjecture, as we have no knowledge whatever of the function of these organs. The lateral line system is very probably for the function of equilibration (see especially Lee, '98) and this would account for its ramifications to the extreme dimensions of the body. The terminal buds are also probably ectodermal in origin. If they arose first as gustatory organs, their migration inwards in the stomodæum toward the tongue and teeth is intelligible. Whether

¹ Subsequent study of the cat fishes confirms this for the siluroids also (Aug., 1900).

the others retained this function or became tactile organs, their migration to the exposed surfaces of the body (barblets, fins, etc.) is equally intelligible.

It is greatly to be regretted that none of my series of sections is sufficiently perfect in the supra-temporal region to permit me to state the exact distribution of the lateralis fibers which go out with the r. lateralis accessorius. They all appear to be given off with the earlier branches of this nerve, but, as none of these branches could be traced to their ultimate termination, the small pit-organs to which these fibers are probably distributed could not be located. We have seen that all of the pit-organs found in the neighborhood of the supra-temporal canal are supplied by the r. supra-temporalis vagi, while the row extending back from this region to the dorsal fin is supplied by twigs of lateralis fibers from the r. lateralis vagi. This latter point agrees with the condition in *Amia* (Allis, '97) and in *Batrachus* (Clapp, '99).

The occurrence of lateralis fibers in the r. lateralis accessorius of *Gadus* strengthens the possibility that the fibers which I have described as arising from the base of this nerve to supply naked sense organs on the top of the head of *Menidia* may be of the same nature. As I stated in my previous contribution, the innervation of these organs in *Menidia* is not absolutely clear, as I was not able to exclude the possibility that lateralis fibers go out with the facial root of the r. lateralis accessorius. The matter is fortunately not one of great morphological importance, as the occurrence of both types of fibers in any form will simplify the interpretation of other cases in which either or both components may be present.

Thus, the communis component alone may be present as in siluroids, and as in *Petromyzon* possibly, if Cole's suggestion ('98 a) holds good. On the other hand, the reduction of the communis element and the exaggeration of the lateralis element might lead to such a condition as that described for *Batrachus* by Miss Clapp ('99). Here the r. lateralis accessorius evidently receives from its facial root a large number of lateralis fibers which are distributed to lateral line organs in a

dorsal series continuing the main line of the head and in a ventral series under the pectoral fin. No terminal buds are described along the course of this nerve. The condition in *Protopterus* (Pinkus, '94) is probably essentially similar, though perhaps more extreme, for here the nerve *r. lat. c. VII + X* of Pinkus' figures, which might be interpreted as the facial root of the *r. lateralis accessorius*, is described as wholly composed of *lateralis* fibers.

As already stated in the descriptive part, I have not been able to demonstrate any general cutaneous fibers entering the *r. lateralis accessorius* either from the Gasserian ganglion or from the jugular ganglion. Nevertheless the conditions are such that it is impossible to exclude the possibility that a small number of such fibers may enter this nerve from one or both of these sources. In any case we are certain that branches of the *r. lateralis accessorius* effect terminal anastomoses with branches of the *r. cutaneous dorsalis vagi*, as well as with dorsal rami of spinal nerves farther back. Miss Clapp's figure ('99, Pl. XVIII, fig. 13) suggests that the *ramus lateralis accessorius* in *Batrachus* receives important general cutaneous accessions from both facial and vagus roots (especially clearly in the latter case), and this again can be correlated with Strong's discovery in the tadpole of the frog of an extra-cranial general cutaneous anastomosis from the vagus to the *facialis*. The condition which he figures and that figured by Dr. Clapp could both be derived from a case in which the *r. cutaneous dorsalis vagi* effected a broad extra-cranial anastomosis with the trunk of the *r. lateralis accessorius*. In *Batrachus* the *communis* fibers which primarily composed the *r. lateralis accessorius* appear to have been largely replaced by *lateralis* fibers (and probably general cutaneous fibers also). The extra-cranial anastomosis with the vagus may represent the vagal root of the *r. lateralis accessorius*; but if so its *communis* fibers have joined the *r. cutaneous dorsalis vagi*, for the origin of this anastomosis from an intra-cranial vagal ganglion and the course of its fibers beyond the anastomosis with the *accessorius* (as described to me personally by Miss Clapp) show unmistakably that this nerve is chiefly the

r. cutaneous dorsalis. Now, if the distribution area of this nerve were to be shifted forward so that these vagal general cutaneous fibers should accompany the r. lateralis accessorius cephalad from the anastomosis, the condition given in the tadpole would be realized by the exaggeration of this vagal general cutaneous component and the reduction of the communis component which primitively composed the r. accessorius. The significance of the intra-cranial anastomosis from the vagus to the facialis in *Batrachus* (marked *com. VII—X* on Miss Clapp's diagram) is obscure. It may represent an intra-cranial (communis) vagal root of the r. lateralis accessorius or Jacobson's anastomosis, or it may even be the sympathetic trunk between the vagus and facialis. In either of the latter cases there would, however, be two points requiring explanation, viz., its intra-cranial instead of extra-cranial course and its connection with the vagus instead of the glossopharyngeus root.

IV. SUMMARY.

This study extends our knowledge of the exact composition of the cranial nerves to another species and shows that *Gadus* and *Menidia* agree substantially in the composition of the cranial ganglia and rami. We are, accordingly, entitled to infer with still more confidence that this arrangement in its broad outlines is characteristic of the Ichthyopsida as a whole. The chief points of difference between the cod and *Menidia* are presented at the beginning of the third part of this paper.

I have in the main confirmed Cole's results in his recent researches upon the nerves of the genus *Gadus*, except in the case of the facial ganglion and r. lateralis accessorius. The latter nerve is composed chiefly of visceral sensory or communis fibers and it is distributed to terminal buds in the vicinity of the fins. The facial ganglion is entirely distinct from the Gasserian and also from the sympathetic and the cod does not exhibit any evidence that the communis system of nerves in general or the facial (geniculate) ganglion in particular is in a state of transition from a cerebro-spinal to a sympathetic type of nervous structure.

The discovery of a small number of true lateral line fibers in the r. lateralis accessorius has suggested some reflections upon certain cases in the literature whose nerves have greatly puzzled the cranial nerve morphologists, particularly the extra-cranial anastomoses between the facialis and the vagus.

Denison University,

October 21, 1899.

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VI. DESCRIPTION OF FIGURES.

All the figures are drawn from a single series of sections, cut serially $13\frac{1}{2}$ micra in thickness and stained by the Weigert method. The scales at the top and bottom of Fig. 1 indicate the serial numbers of the sections. The numbers in parenthesis in the descriptions of the transections are the serial numbers of the sections drawn, so that the transections can be readily located upon the plot. For ease of comparison, the same conventions are employed throughout as in the figures illustrating the *Menidia* paper.

REFERENCE LETTERS.

- a. c.*—anterior semicircular canal.
amp. ant.—anterior ampulla.
amp. ex.—external ampulla.
b. p. o.—branch of the outer buccal nerve for pit-organs behind the eye.
b. v.—blood vessel.
c.—the general cutaneous component of the truncus hyomandibularis.
cil.—ciliary nerve from r. ophthalmicus superficialis V.
com. oph. sup.—the communis element for the r. ophthalmicus superficialis.
com. t. inf.—communis component for infra-orbital trunk.
com. VII.—communis root of the facialis.
cut. t. inf.—general cutaneous component for infra-orbital trunk.
cut. V.—the general cutaneous component of the trigeminus.
d. lat. g.—dorsal lateralis ganglion of the facialis.
d. l. VII.—dorsal lateralis trunk of the facialis, giving rise to the r. buccalis and the r. ophthalmicus superficialis VII.
d. V.—deep root of the trigeminus.
fasc. com.—fasciculus communis.
Gas. g.—Gasserian ganglion.
Gas. g. ex.—extra-cranial portion of Gasserian ganglion.
Gas. g. in.—intra-cranial portion of Gasserian ganglion.
gen. g.—geniculate ganglion of the facialis.
g. IX.—the ganglion of the glossopharyngeus.
g. VIII.—the ganglion of the auditory nerve.
H. M.—os hyomandibulare.

- hy.*—ramus hyoideus facialis.
H¹.—the branch of the hyomandibular trunk for pit-organs under and behind the eye.
Jac. anast.—Jacobson's anastomosis.
lat. ac.—ramus lateralis accessorius.
l. l. VII.—the lateral line root of the facialis.
lob. inf.—lobi inferiores.
low. in. buc.—lower inner buccal branch of the facialis.
l. rec. VII.—lateralis fibers entering the r. recurrens VII.
M.—metacœle, or fourth ventricle.
m. ad. arc. pal.—muscle adductor arcus palatini.
m. ad. hy.—m. adductor hyomandibularis.
m. ad. man.—m. adductor mandibulæ.
man. V.—ramus mandibularis V.
m. lev. arc. pal.—m. levator arcus palatini.
mot. V.—motor root of the trigeminus.
mot. VII.—motor root of the facialis.
m. r. ext.—external rectus muscle.
mx. V.—ramus maxillaris V.
n. II.—the optic nerve.
n. III.—the oculomotor nerve.
n. IV.—the n. trochlearis.
n. o. i. 9.—branch of outer buccal nerve for the 9th organ of infra-orbital canal.
n. V.—the trigeminus nerve.
n. VI.—the n. abducens.
o. i. 8. to o. i. 11.—lateral lines organs of the infra-orbital canal (Cole's nomenclature).
o. m. 11 and o. m. 12.—the 11th and 12th organs of the operculo-mandibular canal.
op. lob.—optic lobe.
op. s. + hy.—the mixed nerve containing the r. opercularis superficialis and the r. hyoideus of the facialis.
o. s. 5.—the fifth lateral line organ of the supra-orbital canal.
out. buc.—outer buccal branch of the facialis.
out. buc. cut.—general cutaneous fibers accompanying the preceding nerve.
o. V.—apparent origin of the trigeminus.
o. VII.—apparent origin of the facialis.
PO.—post-orbital bones.
p. o. c.—post-orbital canal.
PS.—parasphenoid bone.
psbr.—pseudobranch.
r. a. a.—ramulus acusticus ampullæ anterioris.
r. add.—branch of r. opercularis profundus VII for mm. adductor arcus palatini and adductor hyomandibularis.
r. ad. pal.—branch for m. adductor arcus palatini.
r. a. e.—ramulus acusticus ampullæ externæ.

- r. buc.*—ramus buccalis.
rec. 1, rec. 2, rec. 3.—first, second and third roots of the *r. recurrens* VII.
r. lat. ac.—ramus lateralis accessorius.
r. m. ad. man.—motor branch of trigeminus for, *m. adductor mandibulæ*.
r. man. ext. VII.—ramus mandibularis externus facialis.
r. o. m. 10.—nerve for tenth organ of the operculo-mandibular canal.
r. op.—branch of *r. opercularis profundus* VII for *mm. levator* and *adductor operculi*.
r. oph. sup. V.—ramus ophthalmicus superficialis trigemini.
r. oph. sup. VII.—ramus ophthalmicus superficialis facialis.
r. o. p. l.—branch of *r. opercularis superficialis* VII for opercular pit-lines.
r. op. V.—ramus opercularis V (for *mm. levator arcus palatini* and *dilator operculi*).
r. ot.—ramus oticus.
r. ot. cut.—general cutaneous component of *r. oticus*.
r. ot. l.—lateralis component of *r. oticus*.
r. pal.—ramus palatinus facialis.
r. p. t. VII.—ramus pre-trematicus VII.
r. rec. VII.—the *r. recurrens facialis*, or facial root of the *r. lateralis accessorius*.
r. r. u.—ramulus acusticus recessus utriculi.
r. sac.—ramulus acusticus sacculi.
sac.—sacculus.
SO.—supra-orbital cartilage.
sp. V. t.—spinal V tract ("ascending root of the trigeminus").
st. X.—branch of the *r. supra-temporalis vagi* for the pit-line in front of the supra-temporal canal.
sy.—the sympathetic nervous system.
sy. g.—sympathetic ganglion applied to the facial roots.
t. hm.—truncus hyomandibularis.
up. in. buc.—upper inner buccal branch of the facialis.
utric.—utriculus.
v. lat. g.—the ventral lateral line ganglion of the facialis.
X-lat. ac.—vagal root of the *r. lateralis accessorius*.

PLATE XXI.

Fig. 1. A projection of the trigemino-facial ganglionic complex of *Gadus morrhua* upon the sagittal plane, as seen from the left side, x 28. To simplify the diagram the motor component is omitted and also the sympathetic ganglia and nerves. The general cutaneous fibers in the *r. oticus* and in the outer buccal branch are omitted. The relations of the geniculate ganglion cephalad to the supra- and infra-orbital trunks are indicated diagrammatically. Compare the transections on Plate XXII. The peripheral relations of the lateralis fibers in the *r. lateralis accessorius* are doubtful. In all other cases the diagram expresses observed relations only.

The heavy black outline indicates the position of the brain.

Acustico-lateral system, brown.

Lateral line ganglia, black circles.

General cutaneous system, yellow.

Gasserian ganglion, black crosses.

Communis system, red.

Geniculate ganglion, red crosses.

PLATE XXII.

A series of eight transections through the ganglionic complex figured on the preceding plate, x 23. The planes through which the sections pass are indicated by the numbers following the descriptions, which should be compared with those on the scales above and below Fig. 1.

Fig. 2. Section passing through the exit of the trigeminus and the auditory and the ventral lateral line ganglia (962).

Fig. 3. Section passing through the caudal tip of the geniculate ganglion, the auditory and the two lateral line ganglia (943).

Fig. 4. Section passing through the origin of the first rootlet of the facial root of the r. lateralis accessorius (918).

Fig. 5. Section passing through the second and third rootlets of the same nerve (898).

Fig. 6. Section passing through the caudal edge of the Gasserian ganglion and the cephalic tip of the geniculate ganglion (886).

Fig. 7. Section passing through the middle of the Gasserian ganglion (872).

Fig. 8. Section taken a little farther forward (855).

Fig. 9. Section through the extreme cephalic tip of the Gasserian ganglion (847).

NOTES ON PROF. JUDSON HERRICK'S PAPER ON THE CRANIAL NERVES OF THE COD FISH.

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University College, Liverpool.

I am indebted to the courtesy of Professor Judson Herrick for the opportunity of examining his work on the Cranial Nerves of the Cod Fish before it was sent to the printer, and willingly respond to his considerate invitation for some remarks on those parts of the work that concern myself. Before doing so, however, I must say that, whilst it is very gratifying that he should confirm my work as far as regards the lateral line system, which was the principal object of my paper, it is only doing his work an obvious justice to admit that, by the examination of much older fish by "Markscheidenfärbung," he has made considerable advances as regards two subsidiary but important questions on which I had hoped to have thrown some light. I now beg to add the following notes to his paper:

1. The little twig (Fig. 1, *r. o. p. l.*) is *not* represented in my sections. It must be remembered that the correspondence between the pit-organs of *G. morrhua* and *G. virens* is general, but by no means exact, i. e., applies to *areas* and not to individual sense organs, and the organs innervated by this twig in *G. morrhua* may be absent in *G. virens*. Greater variations than this occur in the lateral line systems of the two species. Note further the absence of the barbule in *G. virens*.

2. Prof. Herrick appears to cast doubt on my statement that the IXth nerve contributes to the lateralis accessorius. However inexplicable this statement may be, there can be no doubt as to its foundation in fact. The connection was not always found, but it *was* found in some cases on removing the roots of the IXth and Xth to a dish, and dissecting them care-

fully under a 1 inch dissecting microscope. T. J. Parker ("Zooomy," p. 125, Fig. A) seems also to have found it.

3. *Facial Ganglion.* In his *Menidia* paper Prof. Herrick says (p. 248 of the reprint, p. 404 in the Journal of Comp. Neurology): "The geniculate ganglion [of *Gadus*] is wholly intra-cranial and so closely joined to the Gasserian ganglion that Cole failed to differentiate them and mistook the extra-cranial sympathetic ganglion for the geniculate." Again, in the memoir now under consideration it is stated that, "this description [of the facial ganglion] was most puzzling to me until I discovered that the 'facial' ganglion here referred to is in reality the sympathetic ganglion." Now, if we refer to my actual statements on this question, we find (p. 136): "When I first recognized it in my sections, and saw that its cells were small and corresponded precisely to the cells in the ciliary ganglion, with which I compared it, *I concluded at once that it must be the anterior sympathetic ganglion of the cephalic system described by the older anatomists*" (italics now added). Again on p. 143: "We have seen that the facial ganglion is a ganglion placed on fibers that undoubtedly belong to the seventh or facial cranial nerve. It seems therefore to belong to the trigemino-facial complex, and cannot, in face of this fact, be considered a purely sympathetic ganglion. But we have further seen that it has many sympathetic characters, for in the first place it is connected with the fibers of the fasciculus communis system, which we know to be essentially sympathetic in character; in the second, its cells are small and correspond to the cells found in the ciliary and true sympathetic ganglia; and in the third, it gives origin to the cephalic sympathetic trunk." These quotations prove that I took up the position that I did with my eyes open, and was *not* guilty of the gross error implied to me. That is to say, I was fully alive to the fact that the "facial" ganglion (which observe, together with the "trigeminal" ganglion, is printed in inverted commas on p. 133) had been described as, and might be, a sympathetic ganglion. In fact my statement of the trigemino-facial ganglia on p. 133 is much the same as Prof. Herrick's except: (1) that he confirms my surmise that the

"trigeminal" ganglion was trigeminal *and* facial; (2) he denies that the facial fibers are connected with my "facial" ganglion; and (3) he states that my "facial" ganglion is a true and not a *partial* sympathetic ganglion, as I had supposed.

Now, apart from the fact that whatever the "facial" ganglion is there is a very strong *à priori* probability that it *does* represent a disassociated portion of the trigemino-facial complex, the really cardinal point is, are any facial fibers derived from its cells? In this connection Prof. Herrick's figures 6 and 7 are not quite as much to the point as I could wish. The fact is that the "facial" ganglion is not only closely opposed to the other ganglia, but that many true facial fibers pass right through the center of the ganglion.¹ It is no explanation of this phenomenon to say that "they appear to arise from it merely because of the way the sympathetic ganglion is crowded up into the foramen among these roots." Why should the ganglion be in that position, and has that position no significance? There are no mechanical necessities explaining it that I am aware of, since in the adult trigemino-facial fibers *do not pass through a foramen at all*, but emerge anterior to the pro-otic, without, in front, any bony or other limitations as to space. Further, I thought my sections *did* show a connection between some of the fibers and the cells—a conclusion which should have been fully verified by other methods of research. But it seems to me that even Weigert sections are also insufficient for this purpose, and I am disposed to consider Prof. Herrick's statement that there is absolutely no connection as "not proven." It is probable that Golgi or methylene blue preparations are necessary to settle this point, and I prefer to suspend judgment pending the production of evidence of that nature, which *may* show that, whilst many or most of the fibers simply pass through the ganglion, others are connected with its cells.

4. With regard to the identity of the branches I described on p. 135, I am unable to be of any assistance with

¹ I take it that Prof. Herrick fully confirms this statement. A *true* sympathetic ganglion occupying such a position may have been described before, but I cannot call an instance to mind.

regard to branches 1 and 2, since I only mentioned them because they passed through the "facial" ganglion. I did not trace their peripheral course carefully. Branch 3 is correctly identified by Herrick. The nerve I referred to as the "pre-spiracular or chorda tympani division of the facial" was dissected carefully on many specimens as regards its proximal course, and was traced on to the lower jaw peripherally. It is lettered H³ in my Fig. 2. Prof. Herrick has shown that it is not the pre-spiracular nerve, and hence cannot be the chorda tympani. Were it not for his statement that the post-spiracular communis component is lacking in *Gadus* (which surprised me after reading his *Menidia* paper), I should have said it was the r. mandibularis internus VII, as he uses this term. I think now it must be the communis fibers in the mandibularis V, although the course of the latter is different from that as observed by me.

5. *Ramus lateralis accessorius*. With regard to this question, it must at the outset be understood that the first *real* demonstration of the communis nature of this system was by Prof. Herrick himself in his *Menidia* paper—a work published after my own. Working on the basis of Strong's paper, I think I was justified in concluding (p. 141, foot-note) that the communis system was a visceral system of nerves. Prof. Herrick still believes that to be the case, and holds that the somatic distribution of the communis fibers has been secondarily acquired. It now seems to me, however, that it may be precisely the opposite that has occurred. If we believe with Dohrn in the gill slit origin of the mouth (a view which has distinctly gained ground lately), and if I am right in saying that the communis fibers are distributed mostly to the mucous membrane of the stomodæal involution and the outer skin, it seems at least as probable that it was originally a cutaneous system, which has, like the early teeth, invaded the mouth. The above statement *re* the communis nature of the accessorius explains our differences as to Baudelot. The essential difference between the two kinds of fibers was not established at the time I was writing, and hence the confusion. Since writing the above, I have concluded that the communis nature of the lateralis accessorius

may have been deduced from Stannius, as well as from the other authors mentioned in the note in my *Gadus* paper. I was, however, so influenced by Strong's paper that I was loth to believe it.

Regarding my statement that the accessorius system is composed of somatic sensory fibers, Prof. Herrick says: "My examination of the literature has led me to no such conclusion, nor can I accept Cole's results as decisive in the matter." To this I only have to say that in spite of Prof. Herrick's demonstration of the communis nature of the accessorius, which I now fully accept, my statement is perfectly correct. If there is to be any uniformity in the use of a term, the term "somatic sensory" must be applied to all sensory nerves distributed to the skin. If Prof. Herrick thinks that it is unwise to apply one term to two systems of fibers of a different character, then his course is to reject the term altogether. He cannot, however, object to *my* legitimate use of it. But if we reject the term, what will this lead to? I do not consider the lateral line system of nerves to fall within the definition of somatic sensory nerves, for the same reason which prevents me from describing the optic nerve as such. They are mostly distributed to structures which, though they are of course derived from the skin, have since acquired other connections and are typically no longer topographical dermal structures. Their nerve fibers moreover are perfectly circumscribed, and do not occur outside of the Ichthyopsida. On the other hand, with regard to the terminal buds, they are truly dermal structures and only represent a section of a multitudinous array of dermal sense organs. For example in mammals we have distinct sense organs for heat, cold, pressure and so on. It is, I believe, now proved that each such class of sense organ has its distinctive nerve fiber. But would Prof. Herrick classify such fibers into a multitude of systems? Such ultimately may be done, but in the mean time it seems a little premature to dogmatize on the subject of nerve components.

One more point. In his *Menidia* paper, p. 42 (of the reprint, p. 198 in the Journal), Prof. Herrick says: "Is the sim-

plicity of the lateral line system in *Menidia* as compared with many other fishes, especially the lower fishes, to be regarded as primitive simplicity or as the result of degeneration? Cole would say the former, for he argues that the naked condition of the sense organs is always the primitive, and that in the decline of the system these organs are lost before the canals. But how about the Amphibia in which the system is fluctuating on the verge of the extinction and yet no canals are present, only naked organs? On the whole, I incline to regard the condition in *Menidia* as reduced, rather than primitive." But can Prof. Herrick produce any evidence to show that the lateral line system *ever was below the surface in Amphibia*? It seems to me that the lateral line organs are characteristically superficial in recent Amphibia, and the fossil forms apparently show the same thing. Moreover, when I state that the primitive lateral line system must have been a superficial one, I do *not* imply the converse, that any fish having superficial lateral line organs has a primitive lateral line system. Further, it is inconceivable that there can be any degradation of a tubular lateral line system which is not set in motion by the degeneration of the sense organs themselves. There are several cases in the literature where it would seem that the sense organs have almost disappeared and left the canals behind. The latter then seem to have varied considerably. On the other hand, *Menidia* may be a teleostean, and therefore a specialized fish, and still have a developing lateral line system, although this would not be expected; or its sense organs may have been reduced both in number and complexity and involved the *consequent* movement of the canals toward the exterior. Prof. Herrick's statement, therefore, that the canals of *Menidia* are degenerate may by no means be improbable.

FURTHER OBSERVATIONS ON THE CONDITIONS DETERMINING THE NUMBER AND ARRANGE- MENT OF THE FIBERS FORMING THE SPINAL NERVES OF THE FROG (*RANA VIRESCENS*).

By IRVING HARDESTY.

(From the Neurological Laboratory of the University of Chicago.)

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 4. Comparison of *Rana virescens* with *Rana esculenta*.
- IX. The Influence of season.
- X. Bibliography.

I. SUMMARY.

1. The results obtained in a previous paper are corroborated in the following particulars :

a). The number of fibers in the ventral nerve root of the frog decreases as the fibers pass from their cells of origin in the spinal cord.

b). The number of fibers in the dorsal root decreases as the fibers pass from their cells of origin in the spinal ganglion.

c). The section of the nerve trunk taken immediately distal to the spinal ganglion (dorsal branches excluded) contains a greater number of nerve fibers than a section of the trunk taken further distal.

These relations are explained as due to growth or to the processes by which a larger frog acquires the greater number of fibers in its spinal nerves than a smaller one.

d). In frogs of increasing weight, the fibers of the dorsal root increase more rapidly than do those of the ventral root.

e). The sum of the fibers in the trunk and dorsal branches combined, exceeds and by a considerable amount, the sum of the fibers contained in the two roots. We assume the addition of fibers on the distal side of the spinal ganglion to correspond to that found on the proximal side, but, owing to the mixing of the dorsal and ventral root-fibers in the distal end of the ganglion, nothing can be demonstrated.

In addition to the corroborated results just enumerated, it has been found :

2. The excess of the sum of the trunk and dorsal branches over the sum of the two roots can not be due to a double counting of the same medullated sympathetic fibers running in the trunk and then passing out in the dorsal branches, because the greater the number of fibers composing the dorsal branches as compared with the number contained in the corresponding nerve trunk, the less does the sum of the trunk and dorsal branches exceed the sum of the two roots. Neither can it be largely due to the splitting of ventral root fibers in the region of the ganglion, for the number of fibers constituting

the excess is in many cases greater than the entire number of fibers in the ventral root.

3. The average percentage increase in the number of fibers per millimeter of length is greater for the dorsal root than for the ventral root.

4. The average percentage increase of fibers per millimeter of length tends to be greater for the trunk than it is for either root.

5. The average rate of growth or increase of fibers per millimeter of length is greater for the smaller specimens than for the larger ones.

6. In proportion to its weight, the smaller frog has a greater number of fibers in its ventral root, dorsal root, and its nerve trunk. In both the large and the small frog the proportions of fibers in the three localities are quite similar.

7. As the animal increases in weight, for each gram gained in weight, it gains in its 6th. spinal nerves alone, about 2.7 ventral root fibers, 4.7 dorsal root fibers and 10.4 fibers in the trunk and dorsal branches.

Thus it may be seen that the frog gains dorsal root fibers more rapidly than ventral root fibers, and, on the other hand, gains fibers on the distal side of the spinal ganglion, more rapidly than in either root.

8. There is a general tendency toward a more rapid addition of fibers during the warmer months of the year. That the results are not more decided, may be due either to the fact that the frogs used in winter were not in the normal hibernating condition, or that some ingrowing fibers may not reach their destination during a single season.

II. INTRODUCTION.

In a previous paper issued from this laboratory,¹ counts were made of the fibers contained in the dorsal and ventral roots and in the nerve trunk and dorsal branches of the spinal nerves of the frog. In case of each nerve, counts were made

¹ Hardesty, I.: *Journal of Comparative Neurology*, Vol. IX, No. 2, 1899.

at the two levels of both the roots and trunk. In case of the roots, counts were made of the fibers contained in sections taken (1) as near the spinal cord as possible with the certainty that the sections were intact; and (2) of sections taken as near the spinal ganglion as would allow them at the same time to be free from spinal ganglion cells. In the longer roots, additional counts were made from sections taken midway between the cord and spinal ganglion. In case of the nerve trunks, the enumerations were made of the fibers in a section taken (1) immediately after the trunk emerges from the spinal ganglion; and (2) of the fibers in a section taken just before the *ramus communicans* appears. Careful counts were also made of the fibers contained in the dorsal branches of each nerve.

The nerves were stained with osmic acid, paraffin sections were made from 3 to 4 micra in thickness, and the counts were made with the application of a photographic method fully described in the former paper.

The following were among the conclusions reached: 1. The number of fibers in the ventral roots decreases as the root passes from the spinal cord towards the spinal ganglion. 2. The same is true for the dorsal root as it passes *from* the spinal ganglion *towards* the spinal cord. 3. A section of the nerve trunk taken close to the spinal ganglion contains (dorsal branches excluded) more fibers than a section of the trunk further distal.

These differences in the number of fibers were interpreted as merely an expression of the manner and rate at which the larger frog acquires, as the result of growth, the greater number of fibers in its spinal nerves.

4. The sum of the fibers in the trunk and dorsal branches together always considerably exceeds the sum of the fibers contained in the two roots.

The material from which these conclusions were drawn was obtained from only two specimens. These differed very slightly in weight and were also taken at about the same season of the year.

Since the publication of these observations, it has been

thought that some interesting and perhaps important light might be thrown on the growth and the arrangement of the nerve fibers as indicated from the examination of the spinal nerves of the two frogs previously employed, if (1) the nerves of a greater number of frogs were investigated; (2) if these were taken so as to differ more widely in weight; and (3) if they were taken also at different seasons of the year. This paper is a record of such an investigation.

III. THE MATERIAL EMPLOYED.

For the purposes stated, it was necessary to use specimens so chosen as to offer a wide range in weights, and at the same time taken at different seasons of the year. Thus, in order not to confuse whatever influence season might have in the growth processes with differences in the rate of growth occurring in frogs of different weights or stages of growth, it was necessary to group the frogs according to weight and let each season be represented by a frog of as nearly the same weight as possible. In this way the frogs employed fall into three groups of body-weight; each group containing specimens taken in five different months of the year. The three groups comprise seventeen different specimens, ranging from 4.7 grams to 78.8 grams in weight. The group of smaller frogs contains seven specimens with weights varying between 4.7 and 10.7 grams. A group of medium sized specimens involves 5 frogs weighing from 21 to 40 grams, and a group of five larger specimens ranges from 48 to 78 grams.

Since it would have been an almost interminable task to make the necessary counts of the fibers contained in the entire ten spinal nerves, even of one side, only one nerve was examined from each frog, it being assumed that one nerve will show most of the relations which could be obtained from an examination of two or more.

Moreover, it was not thought necessary that this one be the largest spinal nerve possessed by the frog.

The 6th. spinal nerve was therefore chosen, both because of its moderate size and because its dorsal and ventral roots are

of greater length*than those of the other smaller nerves. Also the dorsal branches of the 6th. nerve are relatively more abundant than those of any of the four nerves below it. In this respect, it more closely resembles the nerves anterior to it. In order to study the relations of the dorsal branches to the other parts of the nerve, a nerve with numerous†dorsal branches was preferred.

IV. METHODS AND TECHNIQUE.

The frog was chloroformed and the ovaries, if present, were removed. Then the animal was weighed and its weight and sex recorded. The viscera were next removed together with such portions of the body-wall as would be in the way.

Keeping the specimen moist in physiological salt solution, the spinal cord was laid bare from the ventral side and then the whole specimen placed ventral side up, in a petri dish containing salt solution, and resting upon the stage of a dissecting microscope. With the aid of the dissecting lens, the nerve roots were carefully detached from the cord and the cord removed. The nerve trunk was then severed well beyond the ramus communicans, and with small scissors the tissue into which the dorsal branches enter so cut that the branches themselves would be severed, the danger of stretching or breaking them being thus avoided. Then with as little pulling as possible, the whole nerve was removed and placed upon a narrow strip of glass. Making the dissection under the fluid facilitates the operation considerably, in that it obviates any tendency on the part of the nerve to tangle, and prevents adhesion to the dissecting instruments.

The strip of glass with the nerve adhering to it, was next placed under the dissecting lens, and the roots, trunk, and dorsal branches straightened out and so arranged that the subsequent transverse sections of each could be most easily obtained. Any remaining salt solution was then drained off and the strip of glass with the nerve arranged upon it was put in 1% osmic acid for about ten minutes, or until the nerve was fixed sufficiently to hold its shape. Then the nerve was carefully removed

into a vial containing 1% osmic acid and set aside from 12 to 24 hours.

This method has produced very good results for the 6th. spinal nerve at least, and does away with the exposure of the eyes and nose to the fumes of the osmic acid necessary in the method described in the former paper.

The fixing and staining in the osmic acid completed, the specimen was washed in distilled water from 2 to 8 hours. During this period it was brought in a Minot watch-glass under the dissecting microscope, and most of the periganglionic capsule and other adherent tissue carefully dissected away and the peripheral part of the nerve trunk clipped off close to the ramus communicans. Then a camera drawing was made of the nerve under a magnification of eight diameters. This drawing was useful later on. It could be used to show the number and direction of the dorsal branches, the general shape of the nerve, and the position of the ramus. In case of the small nerves after they had been embedded, the drawings were especially helpful in the orientation of the nerve. Also the lengths or distances between the localities from which the sections were taken, could be more easily ascertained from the drawings. After all the free acid had been removed by washing, the specimen was passed through the increasing grades of alcohol, cleared in xylol and embedded in paraffin. The embedding was done in small paper boxes on the sides of which were marked the date, the weight and sex of the animal, and the number of the nerve.

Thus the embedded specimen could at any time be identified with the drawing which was marked in the same manner.

Transverse sections, 4 micra in thickness, were taken from the required localities and mounted, straightened out and fixed to the slide by the albumen water method described in the previous paper. A separate slide was used for each locality. After the balsam had hardened sufficiently, the section best suited for counting was selected and surrounded by a ring of India ink on the cover glass.

In the enumeration of the fibers contained in the sections, two methods were employed.

If the section was too large for the whole of it to come easily into the field of the microscope with a combination of lenses giving about 700 diameters and with the camera lucida attached, the photographic method, devised and first employed in this laboratory, was always used. This method of photographing the section and counting the fibers represented in the photograph by means of a counting machine with an automatic register, and at the same time controlling the counting by having the section itself under the microscope, has been given in full detail in the paper above cited.

When, however, the section was small enough to be sufficiently magnified to separate and distinguish all the smaller fibers and decide cases that would be doubtful under lower powers, and at the same time come well into the field of the microscope, the following modification of the net method was used.

An ordinary net micrometer was placed in an eye-piece magnifying the squares to the desired size, and the eye-piece so adjusted that the lines of the net appeared sharp and black. Then the camera was adjusted and the images of both the nerve section and the net were thrown on a sheet of unruled white paper placed close to the foot of the microscope. Both the projected outline of the section and that part of the net covering it, were then carefully marked out on the paper. Thus resulted a ring transcribed with a series of uniform squares. The camera was then removed and the counting begun.

The number of fibers found in each square in the microscope was separately recorded in the corresponding square on the paper. In cases in which the cross section of a fiber was cut by a line of the net, one of two signs was used to avoid the fiber being counted twice, or its omission. If it was to be included among the fibers in the square under consideration at the moment, a heavy black dot was made on that part of the line on the paper corresponding to that part of the line in the microscope which cut the fiber. If, rather, the fiber belonged

to the adjoining square, a ring was made at the spot where the image of the fiber would fall on the paper, instead of a dot. Since there were seldom more than 15 fibers in a square, the occurrence of border fibers of this kind was not so very frequent and this simple method of dealing with them proved highly efficient.

When all the squares had been counted and recorded on a sheet of paper, the sheet, for identification, was marked with the same label as that of the slide.

The numbers in the squares could now be added at any time, the sum total being the number of fibers contained in the section.

Only medullated fibers or those stained by osmic acid were counted. By the use of osmic acid for this purpose, sections were secured in which doubtful cases as to whether a structure was a medullated fiber or not, were fortunately rare, and the counts made either by the photographic or the net method proved highly satisfactory.

The net method as here employed, avoids any form of auto-suggestion which might give rise to error, for the observer never knows what number he has obtained for a given section until the numbers in the individual squares have been added, and this may be postponed until all the sections from a given nerve have been counted. The results obtained for the different specimens were neither tabulated nor compared till after all the counts had been made.

V. THE GENERAL RESULTS OF THE COUNTING.

The 6th. spinal nerve of one side was taken from each of seventeen specimens. These were killed during the months of January, April, June, September and October, and ranged between 4.7 grams and 78.8 grams. In this locality at least, *Rana virescens* rarely attains a weight exceeding 80 grams after the ovaries have been removed; and the largest are always female.

In the colder months, animals under the normal conditions of winter could not be secured, but had to be chosen instead

from those kept at the ordinary basement temperature of the laboratory. The fact that these were not in the normal state of hibernation has possibly somewhat influenced the result attained. In most cases, the frogs of a given month were taken at the same time. Occasionally, however, frogs of all the weights required, could not be obtained within the same week.

The reference numerals of Figure 1, mark the levels at which the sections were taken. This figure is made from a camera drawing of a typical 6th. spinal nerve.

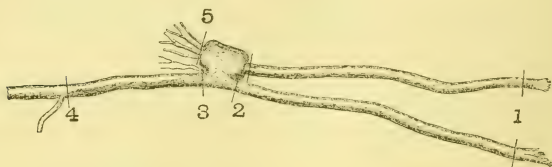


Figure 1.—A typical 6th. spinal nerve of *Rana virescens*. The numerals indicate the localities from which the sections were taken, the fibers in which sections were counted. The sections of the roots were made near the spinal cord at 1 and near the spinal ganglion at 2. Sections of the nerve trunk were taken at the levels indicated by 3 and 4, while 5 marks the locality at which the fibers in the dorsal branches were enumerated. The ramus communicans is shown on the distal side of level 4.

It will be seen that level 1 is near the end of the nerve roots and therefore would be close to the spinal cord, while 2 represents the level at which sections were taken as near the spinal ganglion as possible. Level 3 shows where the first section of the nerve trunk was taken, and 4, where the second section was taken, or the region just before the ramus communicans is given off. Unlike the nerves caudad to it, the 6th. nerve very rarely has more than one ramus communicans. The sections of the dorsal branches were taken at level 5.

Table I contains a record of the number of nerve fibers found in sections taken at the above levels, from a 6th. spinal nerve of each of the frogs mentioned. The entries are made in the order of the weights of the specimens. No attention is paid here to the season during which the nerves were prepared.

This table contains the figures from which were computed all the other tables in this paper.

The reference figures in the headings of the columns of the table correspond with the reference figures of Figure 1, and thus indicate the levels from which the respective sections were taken. The columns of figures are also designated by letters at the top of each column.

The columns in heavier type (columns b and h) contain the numbers by which the fibers were found to vary in the different sections of the nerve roots and trunk taken at the different levels. Column d is obtained by subtracting the sum of the ventral and dorsal roots (column c) from the sum of the trunk and dorsal branches combined (column e), and therefore is the difference between the number of fibers present on the distal side of the spinal ganglion and the number present on the proximal side.

TABLE I.

Month	Body weight in grams	Nerve root	a		b		c	d	e	f	g	h
			Level of the section		Excess at		Sum of roots at	"Distal excess" at	Sum of trunk and dorsal branches at	Fibers in trunk and dorsal branches separate at	Fibers in trunk at	Excess in trunk at
			1	2	2	1	2	3	3	3	4	3
June	4.7	D.	209	223	14		313	80	393	198	188	10
		V.	90	90		0				195		
June	5.1	D.	207	209	2		337	207	544	337	328	9
		V.	131	128		3				207		
January	5.9	D.	252	263	11		391	69	460	237	229	8
		V.	135	128		7				223		
April	7.0	D.	187	193	6		306	75	381	184	175	9
		V.	118	113		5				197		
October	7.4	D.	261	269	8		397	139	536	296	287	9
		V.	129	128		1				240		
September	9.3	D.	215	227	12		370	115	484	264	235	29
		V.	146	143		3				220		
April	10.7	D.	264	273	9		446	112	558	321	305	16
		V.	178	173		5				237		
January	21.6	D.	174	180	6		328	123	461	225	214	11
		V.	150	148		2				236		
June	23.6	D.	302	315	13		508	112	620	363	338	25
		V.	200	193		7				257		
September	25.1	D.	345	353	8		494	223	717	411	392	19
		V.	151	141		10				306		
April	35.4	D.	299	304	5		453	193	646	332	328	4
		V.	154	149		5				314		
October	40.0	D.	368	384	16		575	100	675	456	439	17
		V.	203	191		12				219		
October	48.2	D.	341	350	9		601	244	845	475	469	6
		V.	261	251		10				370		
January	55.3	D.	192	201	9		339	195	534	248	242	6
		V.	139	138		1				286		
June	60.7	D.	423	451	28		618	96	714	438	427	11
		V.	169	167		2				276		
April	61.4	D.	316	326	10		525	141	666	387	374	13
		V.	209	199		10				279		
September	78.8	D.	478	496	18		739	309	1048	689	668	21
		V.	248	243		5				359		

Table I.—The results of the enumeration of the fibers in one of the 6th. spinal nerves of seventeen frogs. The body weight of each frog is given and the month during the frog was taken. The entries are made in the order of body-weight. D, dorsal root; V, ventral root. The entries for the nerve trunk are on the right of the double vertical.

The numbers in the heading of each column correspond to the numbers of Figure I, which mark the levels at which the sections were taken from each

nerve. The columns of figures in heavier type (columns b and h) represent in each case the number of fibers by which a section taken at the one level of a root or trunk exceeds a section taken at the other level.

The numbers of fibers found at the two levels of the dorsal and ventral roots are entered in the double column a, and the number of fibers by which the one section of a root exceeds the other, is, in each case, entered in column b opposite the numbers in column a, which give rise to it. The numbers opposite each other in columns f and g, are the numbers of fibers found in each nerve trunk at levels 3 and 4, and from these numbers, column h, or the variations found for the trunk, are derived. The number of fibers in the respective dorsal branches as taken at 5, Fig. 1, are also recorded in column f, in each case just under the trunk to which they belong. Column e contains the sums of the fibers in the trunk and dorsal branches, and column d contains the various numbers by which this sum exceeds the sum of the two roots as taken at level 2 and recorded in column c.

It will be seen that a section of the dorsal root close to the spinal ganglion or that of a ventral root taken close to the spinal cord, is found to contain more fibers than a section in either case taken farther away. The same is true for the nerve trunk. A section taken in close proximity to the spinal ganglion contains more fibers than are found close to the ramus communicans or at level 4.

It is also shown (column d), that in every case the number of fibers in the trunk and dorsal branches combined is considerably in excess of the sum of those in the two roots. For the sake of convenience the term "*distal excess*" will be used to designate this excess of fibers on the distal side of the ganglion.

Data as to the intimate structure of the region of the spinal ganglion sufficient to adequately explain the existence of the "*distal excess*" are wanting at present. An investigation involving this point is now in progress in this laboratory, and a detailed discussion of the causes giving rise to the excess will best be deferred until this investigation has proceeded further. However, some of the relations of the distal excess to the number and grouping of the fibers in the roots, trunk, and dorsal branches, brought out in the present figures, may be mentioned here.

VI. THE EXCESS OF FIBERS ON THE PERIPHERAL SIDE OF THE SPINAL GANGLION.

This question was touched upon in the previous paper ('99). It was shown there (Tables XI and XII, p. 87) that among the various spinal nerves of a given specimen, those nerves which have the greatest distal excess have also both absolutely and proportionally the greatest number of fibers in their dorsal branches. In other words, the number of fibers constituting the distal excess and the absolute and proportional number of fibers of the dorsal branches tend to coincide. It was seen also that, of all the spinal nerves, the 6th. possesses the greatest proportional and absolute number of fibers in its dorsal branches and therefore shows a greater percentage value for the distal excess than any of the other nerves. For the specimens previously used, it was seen that the distal excess for the 6th. nerve might be as much as 40%. In this series, it will be seen that the 6th. nerve may have a distal excess as great as 61%.

An excess of fibers on the peripheral side of the spinal ganglion has been found by other observers. Birge ('82), made some counts of the fibers in the two roots and nerve trunk of the spinal nerves of the frog. He did not include the dorsal branches at all, and nevertheless found two nerves in which the fibers in the trunk alone exceeded the sum of the two roots. He was at a loss to explain this excess.

Gaule and Lewin ('96) counted the fibers on the central and peripheral side of the spinal ganglion of three of the sacral nerves of the rabbit. They included the dorsal branches and found distal excesses of 11%, 15%, and 19% respectively.

Bühler ('98), in a very interesting paper dealing with the structure of the spinal ganglion cells, in order to compare the number of fibers with the number of cells in the ganglion, counted the fibers present on both sides of the ganglion. The one case in which he reports having done this was that of a 9th. spinal nerve of the frog and there he found a distal excess of 25.5%. Bühler does mention having included the dorsal

branches in his counts. He used *Rana esculenta*, and nothing is known as to how great a distal excess is to be expected for this species. For the 9th. nerve of *Rana virescens*, 25% is quite possible.

More recently, Dale ('00) has made similar counts of the fibers in some of the coccygeal, two thoracic and one lumber nerve of the cat. He reports having found an average excess of only 0.5% on the distal side of the ganglion. Whether Dale included the dorsal branches in making his counts, he does not exactly say. He mentions only the trunk in his tables and the text referring to them, and compares his results with those of Holl, Stienon, and Birge, none of whom did include the dorsal branches.

The 6th. nerve being the only one dealt with here, it is to be assumed that higher distal excesses are found than would be had other spinal nerves been included. The numerical excess found for each of the specimens can be seen in Table I, but in order to present some relations not emphasized in Table I, a special table is given.

Table II contains the numbers (taken from Table I) representing in column 1, the sum of the two roots; in column 2, the sum of the trunk and dorsal branches, and in column 3, the amount by which the latter exceeds the former. In column 4, of this table, given in round numbers are the amounts per cent. by which, in each case, the fibers on the distal side of the ganglion exceed those on the proximal side; i. e., the percentage values of the distal excess. Columns 5 and 6 give an opportunity to compare the relations between the number of fibers contained in the trunk and dorsal branches with the number constituting the distal excess, and column 7 allows a comparison of the number of fibers in the ventral root with the number constituting the excess. The specimens are arranged in the order of their weights. It is seen that in every case the distal excess is large.

TABLE II.

Column	1	2	3	4	5	6	7
Weight in grams	Sum of dorsal and ventral roots close to spinal ganglion	Sum of trunk and dorsal branches taken close to spinal ganglion	Distal Excess	Percentage of distal excess based on sum of two roots	Sum of dorsal branches	Number of fibers in trunk close to spinal ganglion	Number of fibers in ventral root
4.7	313	393	80	26%	195	198	90
5.1	337	544	207	61%	207	337	128
5.9	391	460	69	18%	223	237	128
7.0	306	381	75	25%	197	184	113
7.4	397	536	139	35%	240	296	128
9.3	370	484	115	31%	220	264	143
10.7	446	558	112	25%	237	321	173
21.6	328	461	123	38%	236	225	148
23.6	508	620	112	22%	257	363	193
25.1	494	717	223	45%	306	411	141
35.4	453	646	193	43%	314	332	149
40.0	575	675	100	19%	219	456	191
48.2	601	845	244	41%	370	475	251
55.3	339	534	195	58%	286	248	138
60.7	618	714	96	16%	276	438	167
61.4	525	666	141	27%	279	387	199
78.8	739	1048	309	42%	359	689	243

Table II.—Giving for each specimen, arranged according to weight, (a) the amount of the distal excess and the numbers from which it is determined (columns 1, 2 and 3); (b) the percentage value of the distal excess based upon the sum of the two roots (column 4); (c) the number of the fibers comprising the dorsal branches, the nerve trunk and the ventral root (columns 5, 6 and 7). The table shows first, that the value of the distal excess does not increase regularly with the increase in the weight of the animal; second, that a relatively large number of fibers in the dorsal branches as compared with the corresponding nerve trunk does not increase the value of the distal excess, and third, that in many cases the number of fibers constituting the distal excess is greater than the number in the ventral root.

In the first place the table shows that the increase in the weight of the frog is not accompanied by a regular increase in the percentage value of the distal excess. However, the simple value of the dorsal branches (col. 5) increases more regularly.

If certain architectural proportions are necessary regardless of the size of the frog, it is to be expected of course, that the nerve roots, the trunk and the dorsal branches, should increase in proportion.

It should be noted, however, that while there is no indi-

vidual regularity between the increase in the weight of the frog and the number of fibers forming the distal excess, yet when the entries are separated into three successive groups according to body-weight, the averages for the distal excess show an increase as the animal increases in weight. For the seven smaller frogs, the average distal excess is 114; for the five medium sized frogs, 150, and for the five larger, the average is 197.

It must be remembered that of the total number of fibers contained in all the spinal nerves of a specimen, the proportion of those contained in a given nerve is by no means a fixed one. The two nerves of the same pair even often vary to such an extent that the difference is noticeable to the naked eye. That the number of fibers in the dorsal branches does not increase in the same progression as the animals do in weight is probably to be connected with this fact.

Again, as bearing upon the cause of the distal excess, Table II suggests also that the distal excess cannot be largely due to a double counting of fibers on the distal side of the spinal ganglion. The argument is the following: it is known that fibers from the sympathetic system enter into the spinal nerve by way of the ramus communicans and pass to the spinal ganglion. It is now known also for both mammals and the frog, that some of these sympathetic fibers are medullated, and would therefore be counted as such. The possibility is that some of these medullated sympathetic fibers may neither pass on to the central system nor terminate in the spinal ganglion, but, instead, may pass from the trunk, uninterrupted through the distal portion of the ganglion and out again through the dorsal branches. This being the case such fibers would be counted twice, once in the trunk and once in the dorsal branches. However, if the distal excess were due to the existence of such an arrangement of fibers, then the excess would increase as the number of fibers in the dorsal branches increases. The table shows that for the 6th. nerve at least, the distal excess and the number of fibers contained in the dorsal branches display no tendency to parallel variation (columns 4 and 5).

In the investigation now under way, among other things, an attempt is being made to determine the number of medullated fibers passing between the sympathetic system and the region of the spinal ganglion. A preliminary statement may be here inserted to the effect that, so far, the results show that if all the medullated fibers so passing be included, the number would not be sufficient to account for the distal excess. But even if they were sufficient in number, the canon for mammals at least, is that many of the medullated fibers contained in the ramus are pre-ganglionic fibers, or efferent fibers from the spinal cord which pass from the cord to the sympathetic ganglion by way of the ventral root.

It has been found that a few ventral root fibers divide in the vicinity of the spinal ganglion. One branch may pass through the ganglion and out by the dorsal branches, while the other passes on in the nerve trunk. The author ('99) has observed this for the frog, and a more recent publication of Cajal ('99) pictures the same for the chick. However, a splitting of ventral root fibers cannot to any great extent, contribute to the distal excess. Table II, columns 3 and 7, shows that in many cases the amount of the distal excess is even greater than the number of fibers in the entire ventral root.

Taking the observations altogether, the indications are at present that the distal excess cannot depend on any one set of fibers. The observations point to an explanation based upon the architectural arrangement of the neurones within the spinal ganglion. All the more recent observations on the structure of the spinal ganglion tend to show that it is far more complicated than was at one time thought. It can now be looked upon as partaking the nature of a nucleus of termination as well as containing cells giving origin to the Ranvier T-fibers.

At the present stage of the investigation, it seems probable that the distal excess is due to the following causes :

1. It may to a small extent be due to a splitting of ventral root fibers in the vicinity of the spinal ganglion.
2. To a splitting of the peripheral prolongation of the T-fiber arising from the ordinary spinal ganglion cell,

3. To a greater extent the distal excess may be due to medullated fibers from the sympathetic system which terminate within the spinal ganglion.

4. It may be to a less extent due to the existence of cells in the spinal ganglion which send processes toward the periphery, but not toward the central system.

These statements are based upon observations made both in this laboratory and elsewhere.

VII. THE CHANGES IN THE NUMBER OF FIBERS FOUND AT DIFFERENT LEVELS IN THE DORSAL AND VENTRAL ROOTS AND IN THE NERVE TRUNK.

As has already been stated, counts were made of the fibers present in sections taken at different levels of the two roots and of the nerve trunk. Similar counts were made in the former investigation, but there only two specimens were used, and they differed but slightly in weight. The main object then was to ascertain if possible, the manner and rate at which a given specimen acquires in all its spinal nerves the additional fibers which it is known to acquire as it advances in weight. In the present instance, quite a number of specimens were employed differing widely in weight, and, in order to shorten the task as much as possible, only one nerve was taken from each specimen.

For reasons given above, the 6th. spinal nerve was the one nerve chosen. Sections were taken at the different levels of the two roots and the trunk of this nerve as indicated in Fig. 1.

As already stated, an enumeration of the fibers contained in the sections showed a variation in the numbers found at the different levels of a root or of a trunk. This variation always consisted in the presence of a few more fibers in that section nearest the cells giving origin to the fibers contained in it. These variations found in the roots and trunk of the 6th. nerve are similar to those found in the former paper for the several spinal nerves of one frog.

Bearing on this topic, there is but one other paper to be considered.

Dale ('00) in his investigation above referred to, reports having made a set of similar counts for one of the coccygeal nerves of the cat. His paper deals principally with the number and diameter of the fibers found in single sections of the nerve roots and trunk. However, he states that, in order to test the findings previously published from this laboratory as to the variations in the number of fibers at different levels, he counted "Sections of the roots and trunk taken near the ganglion and again sections at some distance from the ganglion on either side." These counts were for one 4th. coccygeal nerve. He reports having found no variation in the number of fibers either in the ventral root or in the trunk. In the dorsal root he found a few more fibers in the section taken at a distance from the spinal cord than in the one taken near the ganglion—a variation in the opposite direction from that here found in the nerves of the frog. That Dale's result does not agree with the results previously obtained and here extended is probably due to the fact that the growth of the nervous system of the frog is much slower than that of the mammal. The cat has a fixed period of growth while the frog, if it does not grow as long as it lives, at least cannot be said *not* to do so. It cannot be said that any of the specimens here employed had attained their full growth. Further, it is not known whether the fibers in the spinal nerves of the mammals increase in number while the animal is acquiring its extra-uterine growth. It would be interesting to determine whether an adult cat has a greater number of fibers in its coccygeal nerves, for example, than a young kitten. Schiller ('89) counted the fibers in the oculo-motor nerves of three cats at birth, and several at later ages. His averages give the adult cat so few more fibers (3%) than the new-born, as to indicate that this nerve at least, of the cat, early acquires its numerical completeness. It has been amply shown that the nerves of the older frogs contain considerably more fibers than those of the young ones, and one of the purposes of this paper is to determine the rate at which this greater number is acquired.

The roots of the various nerves of a given frog vary greatly

in length, and also, as in the case in hand, the roots of the same spinal nerve taken from specimens of different weights may vary much, both in length and in the number of fibers contained in them. Because of these differences in number and length, the absolute differences in the number of fibers found in the two sections of a root or trunk would mean very little as to the actual rate at which new fibers are growing in. Therefore, in order to compare the differences in number found to occur between two sections of a small root or trunk taken necessarily close together, with the differences found between two sections of a larger root or trunk taken further apart, it is obvious that just comparisons can only be made by computing the percentage values of the differences in number for a unit of length through which these differences occur.

The first three columns of Table III give the result of such computations for the various specimens employed. Other columns, taken from Table I, contain the figures from which these computations were made. It will be seen that the columns of the table are arranged in sets of three, one column of each set representing the dorsal root, one the ventral root, and one the conditions found for the nerve trunk. Set 3 gives the number of fibers by which the sections taken near the cells giving origin to the fibers contained in them were found to exceed those taken farther away. Set 4 gives the actual numbers of fibers found in the sections taken nearest the cells of origin (in the spinal cord or spinal ganglion as the case may be). In other words, set 4 represents the sections of the roots and trunk found to contain the greater number of fibers and therefore contains the excesses given in set 3. The three columns forming set 2 show the amounts per cent. of the excesses given in set 3, based upon the numbers given in set 4; i. e., set 2 is obtained by dividing the numbers of fibers by which the one section exceeds the other, by the number of fibers in the section containing the excess or the section containing the greater number of fibers. Set 5 gives the lengths between the sections of the dorsal root, ventral root and nerve trunk respectively, or the distances through which the excesses occur. There-

fore the figures of the first three columns are obtained by dividing set 2 by set 5 in order to get the more comparable results of the percentages of the variations in the numbers for each millimeter of the distances through which the variations occur.

TABLE III.

Set		1			2			3			4			5		
		Percentage of excess per mm. of length			Percentage of excess based on the greater number			Excess of the greater number			Greater number of fibers in			Length in millimeters between the sections		
Body weight grams		Dorsal root	Ventral root	Trunk	Dorsal root	Ventral root	Trunk	Dorsal root	Ventral root	Trunk	Dorsal root	Ventral root	Trunk	Dorsal root	Ventral root	Trunk
Small	4.7	4.2	0.0	5.1	6.3	0.0	5.1	14	0	10	223	90	198	1.5	1.5	1.0
	5.9	2.4	2.6	3.4	4.2	5.2	3.4	11	7	8	263	135	237	1.7	2.0	1.0
	7.0	1.0	1.4	3.8	3.1	4.2	4.9	6	5	9	193	118	184	3.0	3.0	1.2
	7.4	1.2	0.3	2.3	2.9	0.8	3.0	8	1	9	269	129	296	2.5	2.5	1.5
	9.3	2.6	1.0	4.4	5.3	2.1	11.0	12	3	29	227	146	264	2.0	2.0	2.5
	10.7	1.1	1.1	2.0	3.3	2.8	5.0	9	5	16	273	178	321	3.0	2.5	2.5
Averages		2.0	1.0	3.5												
Medium	21.6	0.9	0.4	3.3	3.3	1.3	4.9	6	2	11	180	150	225	3.7	3.7	1.5
	23.6	1.2	1.0	2.3	4.1	3.5	6.9	13	7	25	315	200	263	3.5	3.5	3.0
	25.1	0.6	1.7	2.0	2.3	6.6	4.6	8	10	19	253	151	411	4.0	4.0	2.3
	35.4	0.3	0.7	0.4	1.6	3.3	1.2	5	5	4	304	154	332	5.0	5.0	3.0
	40.0	1.0	1.5	1.5	4.2	5.9	3.7	16	12	17	384	203	456	4.0	4.0	2.5
Averages		0.8	1.0	1.9												
Large	48.2	0.6	0.9	0.3	2.6	3.8	1.3	9	10	6	350	261	475	4.0	4.5	4.0
	55.3	0.7	0.1	0.8	4.5	0.7	2.8	9	1	6	201	139	248	6.0	6.0	3.5
	60.7	1.2	0.2	0.6	6.2	1.2	2.5	28	2	11	451	169	438	5.0	5.0	4.0
	61.4	0.4	0.7	0.8	3.1	4.8	3.3	10	10	13	326	209	387	7.0	7.0	4.0
	78.8	0.7	0.4	0.6	3.6	2.2	3.0	18	5	21	496	248	659	5.5	5.5	5.0
Averages		0.7	0.4	0.6												
General Averages		1.1	0.8	2.0												

Table III.—Giving the percentage values per millimeter of length by which the numbers of fibers found in the nerve roots and trunk near the cells of origin, exceed the numbers found farther away. There are also given the figures from which these values were computed.

The entries in the table are arranged in groups and under each group is given the averages of the percentage variations per millimeter of length for that group. The general averages for the whole table are also given.

The table shows, (1) that the percentages are higher for the younger animal; (2) that the values are generally higher on the peripheral side of the ganglion (trunk) than on the ventral side (roots); (3) that in most cases the dorsal root (even of the 6th. nerve) has higher values than the ventral root.

The specimens entered in the table are divided into three groups: a group of small specimens, a group of medium sized specimens, and a group of larger specimens. Under each group are given in their respective columns, the averages for that group.

It is seen by comparing the averages for the three groups that in the nerves of the smaller and more rapidly growing specimens, fibers are being added more rapidly than in the larger specimens of the other two groups. Also, while the differences are not so great, the figures show that fibers are growing into the nerves of the medium sized specimens more rapidly than in the larger specimens.

Again, by comparing the averages it is seen that, for the younger specimens, the percentage rate of increase in the number of fibers per millimeter of length is greater for the dorsal root than for the ventral root and greater for the trunk than for either root. It was shown by the figures obtained by Birge ('82) that when all the spinal nerves are taken into account, the sensory or dorsal root fibers of the growing animal increase more rapidly than do those of the ventral root. For the 6th. nerve, alone considered in Table III, this statement does not hold in case of the medium sized specimens, but is again true for the larger group. This discrepancy is almost wholly due to a single exceptional case in the medium group. The value of the variation found for the ventral root of the 25.1 gram specimen is exceptionally high. The discrepancy would perhaps disappear could all the spinal nerves be included. The distribution of fibers to a given nerve is by no means fixed and this may account for some irregularities in the 6th. nerve.

As to the rate of increase in the trunk, it is seen that the amount by which the trunk exceeds the rate of either root is less for the medium specimens than for the small ones, while for the large specimens the rate for the trunk is even exceeded by that for the dorsal root. This might be considered as due to the ingrowth or medullation of sympathetic fibers taking place with relatively greater rapidity in the trunk of the older frog, but this is not at all probable. It can be shown that med-

ullated sympathetic fibers contribute to the formation of the distal excess, and therefore if these fibers were added more rapidly in the older than in the younger nerves, then the distal excess would be higher for the larger specimens. Table II does not show this to be the case. Indeed if it can be assumed, as is probably the case, that the sympathetic fibers in question acquire their medullary sheaths after they have grown into the nerve trunk, then they would be counted in both sections of the trunk and would not enter at all as a factor giving rise to a greater number of fibers in the one section than in the other.

These medullated sympathetic fibers would, however, affect the percentage values of whatever number of fibers there may be growing into the nerve trunk from the spinal ganglion or ventral root and which have not yet reached the locality of the more distal section of the trunk. They would decrease the percentage values by simply increasing the total number upon which the percentage is based. The table shows that as the animal advances in weight the rate of growth for the trunk decreases more rapidly than that for either root.

Therefore the principal conclusions to be drawn from Table III are (1) the younger or more rapidly growing specimen acquires nerve fibers more rapidly than the older ones; (2) as a whole the rate of growth for the dorsal root is greater than that for the ventral root; and (3) the rate of growth tends to be higher for the trunk or distal side of the spinal ganglion than for the central side, showing that the growth of the trunk cannot depend wholly upon the growth of the two roots.

Another interesting set of growth relations is suggested in Table III but can be best brought out in a separate table.

VIII. THE RELATION BETWEEN THE WEIGHT OF THE FROG AND THE NUMBER OF FIBERS CONTAINED IN ITS SPINAL NERVES.

That the larger frog possesses the larger spinal nerves is a matter of simple observation. The relations, however, between the gain in weight and the increase in the size of the nerve were first investigated, for the frog at least, by Birge ('82).

He investigated the matter only as far as the gain in the number of fibers contained in the ventral roots is concerned. He counted the ventral root fibers of all the spinal nerves of one side of six specimens ranging in weight from $1\frac{1}{2}$ to 111 grams. Then assuming that the numbers are approximately equal, he doubled the numbers obtained for one side in order to get the entire number of ventral root fibers present in the spinal nerves of both sides. By dividing differences in number of fibers by differences in weight in grams, he obtained in the six specimens, an average of 51 ventral root fibers gained for each gram gained in weight.

He also counted the fibers in the dorsal roots and in the trunks of two of the frogs. His tables show that these frogs weighed 23 and 63 grams respectively. Since Birge did not include the dorsal branches, the figures thus obtainable would not give the required relations for the trunk as here shown in Table III. If, however, the sums of the dorsal root fibers be doubled in each case and the number thus obtained for the 23 gram frog be subtracted from that obtained for the 63 gram frog and the difference in favor of the larger specimen be divided by the difference in weight, there is found a gain of 77 dorsal root fibers for each additional gram in weight.

In this paper unfortunately the 6th. spinal nerve only has been examined and not the entire number of spinal nerves. An attempt was made to estimate the total numbers of root fibers for all the spinal nerves by taking the proportional values of the 6th. nerve, obtainable from Birge's figures, and applying those values to the figures here found. This attempt revealed the fact that the species of frog used by Birge is not at all comparable in this respect with that here employed. The American *Rana virescens* is found to possess a good many more fibers in its spinal nerves in proportion to its weight than the European *Rana esculenta*, the species investigated by Birge. This is not only true when the 6th. nerve is compared with the 6th. nerve of frogs of like weight, but also the numbers previously obtained for the greater number of the spinal nerves of

Rana virescens are found greatly to exceed per gram of weight, the numbers given by Birge.

That *Rana esculenta* has a smaller nervous system in proportion to its body-weight than *Rana virescens* has been shown in another way. Fubini ('81) made a large number of weighings for both *R. esculenta* and *R. temporaria*. His tables compare the weight of the entire central nervous system with the body-weight, and also the brain weight with the body weight. Donaldson and Schoemaker ('00) made a series of weighing and measurements for *R. virescens*. When the proportions between the body-weight and the weight of the brain and spinal cord obtained by them for *R. virescens* are compared with Fubini's results for *R. esculenta*, it is found that *R. esculenta* has a considerably lighter central nervous system in proportion to its body weight than *R. virescens*. Although as shown by Donaldson and Schoemaker, the weights for the spinal cord obtainable from Fubini's tables are somewhat large, yet the weight of the cord alone in proportion to body-weight is less for *R. esculenta* than for *R. virescens*. Fubini's tables show that *R. temporaria* also has a relatively heavier central nervous system than *R. esculenta*.

The relations between the weight of the frog and the number of fibers contained in its 6th. nerve alone may prove of some interest.

Table IV groups the seven smaller specimens ranging from 4.7 to 10.7 grams against the five larger ranging from 48.2 to 78.8 grams. For each specimen is given in separate columns, the number of fibers in each of the roots and the number on the distal side of the spinal ganglion. In order to get the average number of fibers for each gram of weight, the sums of the fibers for each of the roots and for the trunk are divided by the sum of the weights of the specimens in each group. The table also gives the number of fibers the average frog of each group would possess in its 6th. spinal nerve of one side.

TABLE IV.

	Weight in grams	Ventral root fibers	Dorsal root fibers	Trunk and dorsal branches
7 small frogs	4.7	90	223	393
	5.1	131	209	544
	5.9	135	263	460
	7.0	118	193	381
	7.4	129	269	536
	9.3	146	227	484
	10.7	178	273	558
Sums	50.1	927	1657	3356
Averages	7.16	132.4	236.7	479.4
Average No. fibers per gram		18.5	33.0	66.9
Proportions		1	1.7	3.6
5 large frogs	48.2	261	350	845
	55.3	139	201	534
	60.7	169	451	714
	61.4	209	326	666
	78.8	248	496	1048
Sums	304.4	1026	1824	3807
Averages	60.9	205.2	364.8	761.4
Average No. fibers per gram		3.3	5.9	12.5
Proportions		1	1.8	3.8

Table IV.—This table, based upon figures taken from Table I, compares the averages of two groups; one consisting of the seven smallest frogs, the other of the five largest. The table is intended to offer a comparison (1) of the number of fibers the average specimen of each group would possess in the ventral root, dorsal root, and trunk and dorsal branches combined of its 6th. spinal nerve; (2) of the average number of ventral root, dorsal root, and fibers distal to the ganglion possessed by each of the specimens of each group per gram of weight; and (3) the table allows one to compare the proportions existing between the average numbers of fibers per gram of weight found for the three localities of the nerve.

The relations which Table IV is intended to show are the following:

(1) The smaller specimen has a greater number of fibers in proportion to its weight than the larger one.

(2) The number of dorsal root fibers per gram of weight is greater in both cases than the number of ventral root fibers.

(3) As to be expected after considering the distal excess, the average frog possesses a greater number of fibers in the trunk and dorsal branches combined than in the two roots. This shows that the number of fibers in the trunk and dorsal branches has increased more rapidly than in either or both roots.

(4) It is seen that the average numbers of fibers per gram found for the three localities of the nerve respectively are considerably different in the two groups, yet a comparison of the proportional numbers of the one group with the proportional numbers of the other group shows quite a degree of similarity. This similarity in the proportion of ventral to dorsal root fibers and distal fibers indicates a tendency to maintain a certain relation between the numbers during the growth of the animal.

The figures of Table IV, representing only the condition of affairs in the 6th nerve, may be utilized to obtain the relations to be found when all the spinal nerves are taken into account.

The figures of Birge, above referred to, including all the spinal nerves also show that the smaller specimen possesses a greater number of fibers in proportion to its weight than a larger one. This, taken together with the fact that the smaller specimen gains nerve fibers more rapidly than the larger one, no doubt indicates that the subsequent increase in the size of the animal does not consist so much in the formation of new tissue elements to be innervated as it does in the increase in the size of those already formed and innervated. However, newly formed tissue elements may not be the only destination of the added nerve fibers. It is highly probable that new nerve fibers may go to tissue elements already having a nerve supply. Single amphibian muscle fibers have been observed having from two to six nerve terminations on them (Sandmann ('85)). Areas supplied by sensory fibers chiefly may also acquire new fibers as the area grows in extent.

Table V is simply an addition to Table IV and is intended to give the rate at which fibers are gained as the frog gains in weight. The table explains itself and shows that a frog growing from 7.1 grams to 60.9 grams (averages from Table IV) must gain 72.8 ventral root fibers, 128.1 dorsal root fibers, and 282 fibers in the trunk and dorsal branches of its 6th. spinal nerve. If we divide these figures by 53.8, the difference between 7.1 and 60.9, or the number of grams gained, we would get for the 6th. nerve of one side, 1.35 ventral root fibers, 2.38

dorsal root fibers, and 5.24 fibers distal to the ganglion for every gram the animal gains in weight. Doubling these would give 2.70, 4.76, and 10.48 fibers respectively as the approximate figures for the increase of fibers per gram of weight in the 6th pair of spinal nerves.

TABLE V.

	Weight in grams	Ventral root fibers	Dorsal root fibers	Fibers in trunk and dorsal branches
Average of five frogs	60.9	205.2	364.8	761.4
Average of seven frogs	7.1	132.4	236.7	479.4
Differences	53.8	72.8	128.1	282.0
Gain of fibers per gram of weight gained		1.35	2.38	5.24

Table V.—Showing the rate at which the fibers of the ventral root, dorsal root, and trunk and dorsal branches of the 6th spinal nerve of one side increase in number as the frog increases in weight. The weights are those of the average frogs as determined in Table IV. The differences represent the number of grams and the numbers of fibers gained, and the gain of fibers per gram is obtained by dividing the numbers of fibers gained in each locality by the number of grams gained.

The 6th nerve is one of the smaller spinal nerves of the frog. The 2nd, 7th, 8th, and 9th are considerably larger, while the 5th and 10th are more nearly equal to it. The remaining nerves are smaller.

Though the proportional number of fibers contributed to a given nerve is not absolutely constant, yet if we could determine what proportion of the entire set of nerves is generally represented by the 6th, this value (applied) might give us some idea of the relations between the total increase of fibers in all the spinal nerves and the increase of the animal in weight. Unfortunately, the counts formerly made in this laboratory did not include the 2nd and 10th nerves. If the computation be restricted to the remaining eight nerves, however, using the figures obtained in the previous paper (Table I, page 69), we get, of these eight nerves alone, the following values for the 6th nerve:

Ventral root-fibers	Dorsal root-fibers	Fibers in trunk and dorsal branches
5.5%	5.9%	7.2%

By applying these values to the numbers in Table V doubled, we get for each gram the frog increases in weight, an increase for both sides of 49 ventral root fibers, 80 dorsal root fibers and 145 fibers in the trunk and dorsal branches combined. If the 2nd and 10th nerves could be included, the numbers would of course be some larger.

While the results are not comparable, it may be of interest to see what relations exist in the figures of Birge when the 2nd and 10th nerves are excluded. Birge counted both the ventral and dorsal roots of only two frogs. The larger of these was 40 grams heavier than the smaller. If, exclusive of the 2nd and 10th nerves, the sums if the dorsal and ventral root fibers, computed for both sides of the smaller frog, be subtracted respectively from the like sums of the larger, and the differences be divided by 40, it will be seen that for each additional gram of weight, the larger specimen gains 39 ventral root fibers and 58 dorsal root fibers. It is seen that these figures for *Rana esculenta* are lower than the 49 and 80 obtained for *Rana virescens*. The figures give perhaps some notion of the relations existing between the two species.

IX. THE INFLUENCE OF SEASON.

Concerning this important point, very little information has been obtained from the figures. In hibernating animals, it seems probable that growth tends to be periodic. The warm seasons of the year should be conducive to the more rapid growth. During exactly what months this more rapid growth occurs, or whether it occurs at all, has not been determined for the frog. All that can be concluded from the figures here obtained as to the season during which the nerves acquire fibers more rapidly, is shown in Table VI. This table groups the specimens, the 6th nerves of which were investigated, under two seasons. The first includes June, September and October, and the second, January and April. Also in each group, the figures are recorded in sets, each set constituting those obtained for a given month. In each set the specimens are entered in the order of their weights. The table is made up from material

taken from Tables I and III. The figures are those for the percentage amount of variation per millimeter of length obtained in the manner discussed under Table III.

TABLE VI.

Percentage increase of fibers per mm. of length									
Season	Weight in grams	June, September and October			January and April			Weight in grams	Season
		Dorsal root	Ventral root	Trunk	Dorsal root	Ventral root	Trunk		
June	4.7	4.2	0.0	5.1					
June	23.6	1.2	1.0	2.3					
June	60.7	1.2	0.2	0.6	2.4	2.6	3.4	5.9	January
September	9.3	2.6	1.0	4.4	0.9	0.4	3.3	21.6	January
September	25.1	0.6	1.7	2.0	0.7	0.1	0.8	55.3	January
September	78.8	0.7	0.4	0.6	1.0	1.4	3.8	7.0	April
October	7.4	1.2	0.3	2.3	1.1	1.1	2.0	10.7	April
October	40.0	1.0	1.5	1.5	0.3	0.7	0.4	35.4	April
October	48.2	0.6	0.9	0.3	0.4	0.7	0.8	61.4	April
Sums		13.3	7.0	19.1	6.8	7.0	14.5		
Averages		1.5	0.8	2.1	1.0	1.0	2.1		

Table VI.—Gives the percentage variations per millimeter of length from Table III, arranged with reference to the month in which the frogs were prepared. The entries are divided into two seasonal groups and under each group are the averages for the dorsal and ventral roots and trunk. The representatives of a given month are entered in the order of their weights.

The highest set of variations in the dorsal root occurs in June and the next highest in September. Also the highest sets of variations in the trunk occur during these months. Since the spinal ganglion also contributes fibers to the formation of the trunk, it might be said that the figures indicate the spinal ganglion to be more active during these months. Beyond this, there is little conformity between the individual localities for a given month. Taken as a whole, the averages show that there is a tendency to maintain a more rapid ingrowth of new fibers during the season including June, September and October. That the average for the ventral root is somewhat greater for January and April than for the other group is due to one exceptional case in each group. The ventral root of the January frog of 5.9 grams is found to stand exceptionally high, while in the ventral root of the June frog of 4.7 grams, no variation at all is found.

That the results for the influence of season upon growth are no more decided, may be due to two causes.

The January frogs were taken from those which had been collected in the autumn and kept at the ordinary basement temperature. The results for these frogs might have been different had normally hibernating animals been available.

But again, even if growth does cease during the winter months, it is by no means certain that counts made then should show a much less percentage of fibers which have not yet reached their destination than counts made during other months. Fibers which start in the warmer months may not complete their extension during those months and thus, though checked during the colder months, would still affect the counts made during this season.

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ANASTOMOSIS OF NERVE CELLS IN THE CENTRAL NERVOUS SYSTEM OF VERTEBRATES.¹

By N. WORTH BROWN.

With Plate XXIII.

In the *Journal of Experimental Medicine*, Vol. V, Nos. 5 and 6, there appeared an article by Martin Fischer upon anastomosis between cells of the central nervous system. This line of investigation being an interesting one and the existence of anastomoses being so often denied, the attempt was made in our own laboratory to demonstrate in lower vertebrates the relations discovered by Fischer in mammals. Some very satisfactory results were obtained and the returns rewarded us for the labor expended. Anastomoses were found in sufficient numbers to satisfy us that they were not mere accidents, that each occurrence was more than a freak of nature and that this type of connection bore some direct relation to the intricate reflex activities of the nervous system.

Preparations were made by Nissl's method from the minnow (*Pimephales notatus* Raf.), the cat, the mouse and the frog and anastomoses were found in both medulla and spinal cord.

Some difficulty was found at first in arriving at the correct degree of differentiation. Sections which were excellent for the study of the internal cell structures were too faintly stained to enable one to follow, for any distance, the processes; those too darkly stained were quite as unserviceable since the precipitate of stain prevented the observer from discerning between relations of mere contiguity and those of actual protoplasmic continuity. When correctly stained the internal structures could be

¹ Studies from the Neurological Laboratory of Denison University, under the Direction of C. Judson Herrick. No. XII.

recognized and the processes followed until they left the plane of the section. The nucleolus appeared as a dark spot within the lighter nucleus; Nissl bodies could be seen not only in the cell bodies but throughout the entire length of the protoplasmic bridges; fibrilar structures could be discerned both in and around the nucleus and in some instances extending from one cell to another.

In one case (Fig. 5) two cells were joined in a manner which suggested a degree of incomplete anastomosis. The two cells and the connecting process being in the same plane, the line of refraction, near the most central cell of the group, (at the point *A*) could not have been caused by a process entering the cell-body at a higher or lower level or by one which passed over or under the cell. The line of refraction may represent the meeting of the protoplasm of one cell with that of the other without as yet having become homogeneous with it.

While examining some old Golgi preparations we were pleased to discover a few cases of anastomoses in the cerebral cortex of the cat (Fig. 6).

In staining with methylene blue the method employed was that used by Fischer, slightly modified to suit the various tissues. The method used by us was:—

(1) Harden in

10% solution of Formalin	24 hrs.
90% Alcohol	24 hrs.
100% Alcohol	3 or 4 hrs.

(2) Embed in paraffin.

Section, 15 to 25 microns in thickness.

(3) Stain with Grüber's methylene blue solution:

Methylene blue	4 parts.
Venetian soap	2 parts.
Distilled water	1000 parts.

Frog tissues for 24 hours; fish, cat and mouse tissues for 48 hours.

(4) Rinse in distilled water, differentiate in anilin oil and alcohol.

Anilin oil	1 part.
Alcohol, 90%	9 parts.

(5) Clear in oil of origanum, rinse in xylol, and mount under cover-glass in damar balsam.

In our experience the tissues of the frog differentiated much more rapidly than did those of the mouse and cat. The frog tissues were also impregnated with the stain in less time than were the others.

Granville, Ohio, June 14, 1900.

DESCRIPTION OF FIGURES.

PLATE XXIII.

Fig. 1. *Pimephales notatus*. Cells in the nucleus of the VI nerve, medulla oblongata. Cells are situated on the opposite sides of a bundle of nerve fibers. $\times 1800$.

Fig. 2. *Pimephales notatus*. Cells of the tuberculum acusticum, under the cerebellar crest, just laterally of the communis root of the VII nerve at the point where it begins to turn outward towards its superficial origin. They are therefore probably cells of the sensory terminal nucleus of the acustico-lateral system of nerves. $\times 800$.

Fig. 3. *Pimephales notatus*. Small cells in the lateral part of the medulla oblongata at the level of the exit of the V root and lying immediately ventrally of the motor nucleus of the V nerve. $\times 2500$.

Fig. 4. Cat. Between the dorsal and ventral horns, in the region of transition between the first segment in the spinal cord and the medulla.

Fig. 5. Cat. Cells in the first segment of the spinal cord between the dorsal and ventral horns. Exhibits at *A* a line of demarcation between two cells which seem otherwise in intimate union.

Fig. 6. Cat. Golgi preparation. Cells in the cerebral cortex, near the lateral fissure.

A BRIEF SUMMARY OF THE RESEARCHES OF THEODORE KAES ON THE MEDULLATION OF THE INTRA-CORTICAL FIBERS OF MAN AT DIFFERENT AGES.

By HELEN BRADFORD THOMPSON.

(From the Neurological Laboratory of the University of Chicago.)

The detailed knowledge which we now possess of the development of the intra-cortical fiber systems of the human brain from birth to adult years, is largely due to the extended and painstaking researches of Theodore Kaes. The results of Kaes's investigations have appeared in a series of papers in German periodicals, extending from 1891 down to 1900.¹ Since this extremely valuable material is not, in its present form, easy of access to English students, it seemed worth while to present in these pages, a concise summary of Kaes's results so far as they have appeared.

The task which Kaes set himself, was that of determining the number and the distribution of the medullated fibers of the various regions of the cerebral cortex at successive ages, from birth to adult years. He assumes the truth of the proposition that the appearance of the medullary sheath means the beginning of functional activity in the neurone to which it belongs. If this be granted, it becomes possible to determine by means of the medullation the period at which each of the various groups of intra-cortical fibers becomes functional, and the length of time that functional development continues within each fiber system. The importance of ascertaining these facts is threefold: 1) it furnishes a basis for correlating intellectual growth with the growth of the brain; 2) it serves as a standard for

¹ See Bibliography.

comparing brains of abnormal individuals with those of normal individuals; and, 3) it opens the way to an important advance in comparative anatomy—the comparison of intra-cortical fiber structure throughout the vertebrate series. The material examined by Kaes with a view to the solution of his problem comprises eleven human brains. Seven of them were those of normal individuals belonging to the laboring class of the German race. Their ages were 1¼; 18; 38; 42; 45; 45; and 53 years. Two of the four remaining brains were those of Asiatic seamen, one a Chinaman and one a Hindu, each about forty years of age. The remaining two brains were abnormal—one that of an idiotic dwarf, 25 years of age; and the other that of a microcephalic child of 2½ years.

The brains were all prepared according to the same general method.¹ They were divided into twelve frontal sections and cubical pieces of cortex were taken at various points from each section. These pieces of cortex were prepared according to Wolter's method²—a method which stains the medullated fibers gray or black, leaving the other cortical substance yellow.

Two general methods of examining the sections were pursued, one macroscopic and the other microscopic. The macroscopic method consisted in noting the prevailing color of each section. Since in the stain used the medullated fibers appear gray and all other substance yellow a region which is very rich in medullated fibers appears a uniform gray; while one that is entirely lacking in medullated fibers appears pure yellow. The regions which contain mixtures of medullated fibers and other cortical substance, appear various shades between pure gray and pure yellow. Kaes distinguished five color grades in the

¹ 3, p. 4-5.

² 1, p. 3.

Note—The References to Kaes's papers are given by means of the numbers of the papers in the bibliography at the end of this article. The page numbers given refer in every case to the paging of the reprints, and not to the paging of the periodicals in which the papers originally appeared. The attempt is made to refer each important statement used in the summary to the exact page of the article from which it was taken.

adult cortex—"pure yellow;" "more yellow than gray;" "yellow-gray;" "more gray than yellow;" and "pure gray."¹ Each of the various regions examined was classified under one of these colors. In dealing with the 1¼ year child cortex, this classification could not be applied, because the child cortex appears pure yellow to macroscopic observation in all regions. Differences in shade which offer a basis for an analogous treatment of the child cortex, do, however, occur in the medullary center, which, in the adult is a uniform gray. The shades distinguished in the medullary center of the child were, "light gray," "gray," "blackish," "black," and "deep black."²

The microscopic investigation consisted in noting the number of distinguishable layers differentiated by the stain in each region, measuring the thickness of each layer and recording the characteristics of the fibers composing each layer.³

The general result of the macroscopic investigation was to show that the development of intra-cortical fibers continues much later in life than had previously been supposed. In the child brain, the cortex is uniformly yellow, showing an almost complete lack of medullated fibers. A comparison of an 18-year cortex with a 38-year cortex showed that there was 50% less of the pure yellow substance in the 38-year cortex than in the 18-year cortex, and 50% more of the "more-gray-than-yellow," and "gray" substance, indicating a marked development in the number of intra-cortical fibers between 18 and 38 years.⁴ The microscopic investigation revealed an increase in the number of functional fibers up to the age of about 45 to 50 years.⁵

The more important and detailed results come from the microscopic investigation. Kaes divides the fibers of the cortex into three main typical layers, which are characteristic of all

¹ 3, p. 35; p. 64.

² 5, p. 30; p. 50.

³ 3, p. 5; pp. 8-33.

⁴ 3, p. 35; 2, p. 2.

⁵ 4, p. 2; 6, p. 5.

regions.¹ They are, in his terminology, 1) the zonal layer; a thin layer appearing at the surface of the cortex; 2) the layer of the fibers of the II and III Meynert layers, a thick layer lying just below the zonal layer; and, 3) a thick innermost layer, called the "Outer Association layer," because it is *outer* with reference to the association fiber systems with which Meynert dealt.² Beside these three principal layers, there is one very important stratum of fibers which Kaes classes as a part of

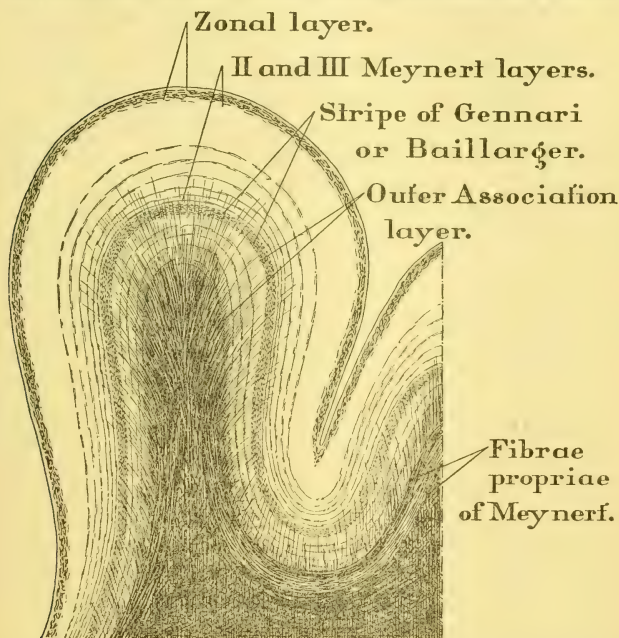


Figure 1.—Semidiagrammatic representation showing the arrangement of the cortical fibers in a section of the occipital cortex of a male child of 1¼ years. From Theodore Kaes, 1894.

The designations used are the same as those in Kaes' papers.

¹ 1, p. 2; 3, pp. 6-7.

² 8, p. 3.

the outer association layer. It is found at the ectal border of the outer association layer, where this meets the II and III Meynert layer. This stratum is named differently according as it appears in the occipital region or elsewhere. In the occipital region it is called the layer of Gennari; in all other regions the layer of Baillarger.¹ At some points in the cortex, this layer is doubled. In connection with these intra-cortical layers, Kaes also treats the Meynert band of *fibræ propriæ*. (See Fig. 1.)

The general course of medullation of the fiber systems of the cortex is described by Kaes in detail. The account of the period earlier than $1\frac{1}{4}$ years, Kaes derives from Vulpus' work but the description of the process subsequent to that time is based upon his own investigations. The first of the fibers connected with the cortex to become medullated, are the projection fibers. At birth they appear raying out almost as far as the cortex. At about four months after birth the very first of the cortical association fibers, the *fibræ propriæ*, become medullated.¹ By eight months the first of the intra-cortical fibers begin to appear in the most advanced regions.²

The description of the further development cannot be accurately assigned to definite ages, partly because some regions of the cortex develop so much more rapidly than others, and partly because Kaes examined no brains between the ages of $1\frac{1}{4}$ and 18 years, nor between 18 and 38 years. A general description of the course of development can, however, be derived from a comparison of the different stages of advancement within the same brain. The first intra-cortical fibers become medullated shortly after the *fibræ propriæ*. They appear as a few scattered fibers running parallel to the layer of *fibræ propriæ* on its ectal border. Gradually these fibers increase in number, spread for a short distance toward the surface of the cortex, and assume a stratified appearance. This is the outer association layer.³ Before the formation of the outer association layer is

¹ 3, p. 43; 1, p. 2.

² 5, p. 41, 44.

³ 5, p. 45; 6, p. 11; 8 p. 3.

completed, two other sets of fibers appear. One of them is found surrounding the outer limit of the projection fibers, which by this time have completed the normal extension of their medullation in the cortex. This is the Baillarger or Gennari layer. It marks the ectal border of the outer association layer, but is composed of coarser fibers than the rest of the layer.¹ The second set of fibers which appears at this period is the zonal layer, at the ectal border of the cortex.² It also is composed of coarse fibers. It is the stage of development just described which is characteristic of the advanced portions of the cortex of the child of a year and a quarter. Its distinctive features are, in brief, a partly developed outer association layer, consisting of some stratified fibers lying next the fibræ propriæ, and the Baillarger layer at its ectal border. These two portions of the outer association layer are separated by a region where the fibers of the layer are yet unmedullated. The Baillarger layer is separated on the other side from the zonal layer, by a space devoid of medullated fibers—the region of the future II and III Meynert layer.

As the process of development continues, the fibers of the outer association layer spread gradually toward the Baillarger until they reach it.³ At the same time the Baillarger and zonal layers grow thicker and richer in fibers. The next stage is marked by the appearance of the inner Baillarger layer and the first fibers of the II and III Meynert layer. The inner Baillarger layer appears as a narrower line of coarser fibers among the finer fibers of the outer association layer, just ental to the outer Baillarger layer.⁴ The fibers of the II and III Meynert layer are the finest of the cortex. The first of them to become medullated are those lying next to the outer Baillarger layer. The general course of development of this layer is, like that of the outer association layer, a gradual spreading of the medulla-

¹ 5, p. 45; 8, p. 3; 6, p. 11.

² 6, p. 11; 8, p. 3.

³ 5, p. 45.

⁴ 6, p. 11.

tion from its ental to its ectal portion. This process continues until the medullated fibers of the II and III Meynert layer meet those of the zonal layer.¹ The final stage in the development of the cortex is the addition of a secondary system of fibers to the primary system just described. The secondary system is entirely composed of coarse fibers. They are first seen scattered throughout the outer association layer. Shortly afterward the same sort of fibers are found in the II and III Meynert layer—at first singly, and later organized into a thin stratum which Kaes calls the “Bechterew streak.” Still later very coarse fibers appear also in the Baillarger layer, and in the most highly developed cortex known, they are found as a secondary system of coarse fibers extending from the ental to the ectal border of the cortex.² Very few regions of the cortex reach this highest stage even in the completely developed adult. The period from youth to maturity is in general characterized³ by the gradual growth of the II and III Meynert layer and the formation of the secondary fiber systems, but even in the fully developed brain there are regions which do not reach the stage at which the II and III Meynert layer exhibits medullated fibers.

The final stages of development reached by any region may be estimated in either of two ways: either by the thickness of the cortex as a whole, and of its constituent layers; or by the complexity of its medullated systems. The determination of the degree of development by cortical thickness is somewhat complicated by a fact to be dwelt upon later, the fact that during the growing period of youth, a thinner cortex means greater development, but that after the cessation of body-growth a thinner cortex means less development. The point at which this change occurs for those regions which reach the highest development, is about eighteen years, but for the less advanced regions, thinning of the cortex

¹ 3, p. 42.

² 6, p. 11-12; 4, p. 2; 8, p. 4.

³ 6, p. 5.

continues to indicate greater development much later than this period.¹ In spite of this difficulty in interpretation, Kaes is able to deduce from his measurements the general statement that in the adult brain the occipital region is the most highly developed of any, the central region is a close second, the temporal is third, although wide variations are found in it in different individuals; the parietal region is fourth and the frontal region is fifth.²

The determination of degree of development by the complexity of the fiber systems gives almost the same result. Both the occipital and the central regions reach the most complete form, in which the Baillarger and Gennari layers are doubled, and the system of secondary fibers appears.³ The fact that the doubled Baillarger and the secondary fiber system are more marked in the central region would indicate that it is somewhat farther advanced than the occipital region,⁴ while the measurements placed the occipital region first. The temporal region, which came third in the measurements, shows such wide variations of fiber systems in individuals of the same age that it is difficult to place it. The posterior frontal region is only a little behind the central regions. In it both Baillarger layers are medullated and the system of secondary fibers has begun to appear. The parietal region is somewhat behind the posterior frontal. The Baillarger layers are less well marked and there are but a few traces of the secondary fibers. The anterior frontal region, although it develops very late, finally reaches about the same stage as the parietal. The Island remains in a very rudimentary condition throughout life. It never gets beyond the point at which the zonal and Baillarger layers first appear. Its II and III Meynert layer never becomes medullated. The gyrus fornicatus is the least developed of any of

¹ 6, p. 4; 11, p. 1.

² 6, p. 6; 5, p. 35.

³ 4, p. 2.

⁴ 6, p. 13-14.

the cortical regions. It contains no Baillarger layer, and only traces of a zonal layer.¹

Kaes nowhere gives a detailed statement of the stage of development reached by each of the regions at different ages, but a general outline of the facts can be gathered from his various papers. The occipital and central regions are the first to attain any completeness in their medullated fiber systems. In the child of 1 $\frac{1}{4}$ years, both regions have reached the point at which the Gennari and Baillarger layers are well marked, and the II and III Meynert layer shows its first medullated fibers.² By 18 years all the primary fiber systems of both regions are filled out.³ The further course of development consists in the addition of new fibers to the primary system, principally in the II and III Meynert layer,⁴ and the development of the secondary fiber system. By about forty years, the central region reaches its highest stage of development, in which the secondary fiber system is continuous throughout the cortex.⁵

The occipital region exhibits its highest stage of development somewhat later. The second Gennari layer and the system of secondary fibers are first apparent in the fifty three year brain, and even at that age, the secondary system is not complete.⁶ The posterior frontal region is also well developed in the 1 $\frac{1}{4}$ year child. The other regions are all in a very rudimentary state at this period. None of them have reached the point at which the Baillarger layer appears. Most of them continue to develop slowly throughout life, finally reaching the point described as the limit for each. The anterior frontal region, however, is at a standstill from childhood to about forty-two years, when the Baillarger layers appear. From this time on to fifty-three it years shows a marked development.⁷

¹ 6, pp. 12-14.

² 4, p. 2; 6, p. 14.

³ 5, p. 37, p. 47.

⁴ 3, pp. 38-45.

⁵ 6, p. 5.

⁶ 6, p. 14.

⁷ 6, p. 13.

Kaes regards the method of measurement as the most exact procedure in determining the growth process of the cortex. It consists in recording the thickness of the cortex as a whole and of each of its constituent layers at successive ages and in the various regions. The most striking fact revealed by the method of measurement is that the cortex of the $1\frac{1}{4}$ year child is very much broader, or thicker, than that of the adult. The average thickness of the child's cortex is 6.5 mm., that of the 18 year adult 3.63 mm., and the average adult 4.94 mm.¹ Comparing the average thicknesses of the cortex for the successive ages, Kaes discovers this general relationship between cortical thickness and stage of development. The undeveloped child cortex is thickest of any. From childhood to youth—about 18 years, the cortex grows gradually thinner as it increases in complexity. It is thinnest during the period of youth.²

From youth to about 53 years, there is a gradual increase of thickness, due to the addition of new fibers. Up to the period of youth, therefore, thicker cortex means a lower stage of development. Beyond the period of youth, thicker cortex means a higher stage of development.³ The process by which the initial thinning of the cortex takes place is, according to Kaes' account, as follows.⁴ The boundary line between the cortex and the medullary center, is marked by the layer of *fibræ propriæ*. In making the measurements Kaes reckoned the *fibræ propriæ* as part of the medullary center, and not as part of the cortex. The portion which was measured as cortex, was therefore that which lies between the pia on one side and the ectal border of the *fibræ propriæ* on the other. In the process of development the medullary center spreads outward on either side through the addition of new projection fibers and

¹ 5, p. 32; 6, Tabella I.

² It must be remembered that Kaes's statements are based upon a series of brains which contains none between the ages of $1\frac{1}{4}$ and 18 years, nor between 18 and 38 years.

³ 6, p. 4; 8, p. 3.

⁴ 5, pp. 32-33; 8, p. 3.

fibrae propriae. Thus the ectal border of the *fibrae propriae*—which is also the ental border of the cortex—is shifted toward the surface of the gyrus, and the portion measured as cortex grows thinner, while the medullary center grows broader. This is the general nature of the process by which the reduction in cortical thickness from childhood to youth takes place. When we turn attention to the details of the process and inquire what changes occur in the separate layers, we are met at the outset by the statement that the outer association layer of the child is of about the same thickness as that of the youth, while the II and III Meynert layer is several times as thick. The explanation offered for this relationship rests primarily upon the method of determining the boundary between these two layers at different stages of development. As we have said in the general description of the course of development, the first of the intracortical fibers to become medullated are the most ental fibers of the outer association layer. They appear as finer fibers forming a brief continuation of the *fibrae propriae* toward the surface of the cortex. Very early this layer of fibers reaches a thickness approximately equal to that of the outer association layer of the youth. Now as development proceeds, the spreading of the medullary center already described pushes the ectal border of the layer of *fibrae propriae* towards the surface of the cortex, while at the same time the ectal border of the outer association layer continues to move toward the surface because of the gradual medullation of its fibers. Thus the ental and ectal borders of the outer association layers move simultaneously in the same direction, and we observe the phenomenon of a shift of the entire outer association layer toward the surface of the cortex, without any appreciable change in the thickness of the layer itself. But during this process, all the distance between the ental border of the zonal layer and the shifting ectal border of the outer association layer is measured as the II and III Meynert layer.

The consequence of this procedure is that we have at first a very diproportionately broad II and III Meynert layer, which is gradually reduced in thickness by the shifting of the outer

association layer toward the surface. This explains how it is possible that the reduction in cortical thickness, although primarily due to a spreading of the medullary center, should show itself in the measurements as a thinning of the II and III Meynert layer. But the appearance of the Baillarger and Gennari layers fixes a permanent boundary between the outer association layer and the II and III Meynert layer.¹ From that point on, Kaes tells us the II and III Meynert layer and the outer association layer of the child measure about the same as, or a little less than, those of the adult.²

The method of measuring the whole unmedullated portion of the cortex between the zonal layer and the partially formed outer association layer as II and III Meynert layer, makes the measurements for the early stages somewhat misleading. But aside from this fact, Kaes' description of the course of cortical development might pass unquestioned, if his measurements fitted his description, but there are several discrepancies between the two which are difficult to reconcile. The most obvious of these is one that comes out in the relation between the thickness of the cortex, and that of the medullary center. The child cortex is given as broader than the youth or adult at all three levels, summit, sides and bottom of the gyrus.³ Measured through from side to side, the total thickness of any gyrus would, of course, be equal to the thickness of the medullary center, plus the thickness of the cortex on either side of the center. Since the thinning of the cortex has been explained as the result of a spreading of the medullary center, if we suppose that the gyrus remains the same size from childhood to youth, then the thinning of the cortex in the youth would be exactly equal to the increase in the breadth of the medullary center. If the gyrus increases in size in the youth, the increase in the breadth of the medullary center would have to be enough to account not only for the thinning of the cortex, but also for

¹ 5, p. 32.

² 5, p. 33.

³ Tables 5, pp. 32, 34.

the increased breadth of the gyrus. The only hypothesis on which the decrease in the thickness of the cortex could be more than the increase in the medullary center, is that the gyrus as a whole should decrease in size from childhood to youth. The measurements which Kaes gives for the breadth of the medullary center and the thickness of the cortex at the sides of the gyrus in the child and 18 year brains are—child cortex 4.9 mm., 18 year cortex, 3.18 mm.; child medullary center 2.73 mm., and 18 year, 2.91 mm.¹ The difference between the thickness of the child cortex and that of the youth is 1.72 mm., on each side of the gyrus, or 3.44 for both sides. If the thinning of the cortex is to be explained as a spreading of the medullary center toward the surface of the gyrus, we should expect to find the 3.44 mm. reduction in the cortical thickness at the sides of the gyri, accompanied by at least an equal increase in thickness of the medullary center. But the medullary center of the child brain measures 2.73 mm., while that of the 18 year brain measures but 2.91 mm. The difference is only .2 mm., instead of about 3.5 mm., as we expected to find it. The only hypothesis on which these measurements could be reconciled is, as we have seen, that the total gyrus grows thinner from childhood to youth—a supposition which seems very improbable. Kaes nowhere recognizes that such a result follows from his tables of measurements, nor does he mention any process by which the total size of the gyrus could be reduced during the period of growth.

It will be remembered that in the description of the growth process of the fiber systems of the cortex the statement was made that the reason the II and III Meynert layer seemed so disproportionately broad in the child cortex, was that all the space between the zonal layer and the ectal edge of the developing outer association layer was measured as II and III Meynert layer.² But with the appearance of the Baillarger layer, the permanent boundary line between the II and III Meynert layer and the outer association layer was fixed, and from this

¹ 6, Tabella I. 5, p. 32, table.

² 5, p. 33.

time on the II and III Meynert layer of the child measured about the same as, or a little less than, the adult.¹ In fact the most significant growth process in the later periods was stated to be the increase in the thickness of the II and III Meynert layer due to the addition of new medullated fibers. In the description of the cortex of the child, Kaes states that the occipital region and possibly also the central region have reached the stage of development in which the boundary line between the II and III Meynert layer and the outer association layer is fixed by the medullation of the Baillarger and Gennari layers.²

At these points, therefore, we should expect to find that the II and III Meynert layer of the child measures a little less than that of the youth or adult. But the tables of measurements for the child cortex give a thickness for the II and III Meynert layer of these regions which is more than twice as great as that of the youth or adult.³ No attempt is made to reconcile this discrepancy between the tables and the descriptive statements, nor is any process mentioned which could account for a thinning of the II and III Meynert layer subsequent to the appearance of the Baillarger and Gennari layers.

The comparison of the Chinese and Hindu brains with the German revealed no very marked differences of fiber stratification. The general impression gained from the preparations was that in the Asiatic brains, the fibers are coarse and less numerous, while in the German brains they are fine and more numerous.⁴ The measurements showed that both the Hindu and the Chinaman were below the Germans in their development. The difference was most marked in the case of the Hindu.⁵ His brain had a medullary center which was narrower than that of the German, and a cortex which was broader. In both these respects the Hindu brain resembled that of the child, rather than that of the

¹ 5, p. 33.

² 5, p. 35-37.

³ 5, p. 36 table.

⁴ 6, p. 14.

⁵ 6, p. 10-14.

adult German. The Chinese brain had a cortex and medullary center which measured about the same as the German. Its lower stage of development was indicated by the fact that the II and III Meynert layer was not so well developed as in the German, while the outer association layer was fully as well developed or better.¹ The same statement holds true of the of the Hindu brain. The under-development of the II and III Meynert layer, and the advanced development of the outer association layer, Kaes regards as very significant, because it is the II and III Meynert layer which develops late in life and is characteristic of the higher stages, while the outer association layer is more primitive. In general the statement would hold good that the Hindu and Chinese brains are most like the German in the poorly developed regions, and less like them in the more advanced regions,² but the gyrus fornicatus presents a marked exception to this rule. In the German brains the gyrus fornicatus is the least developed region. It has not reached the stage at which the Baillarger layer appears. In the Asiatic brains, a well developed system of primary fibers is present in the gyrus fornicatus.³ Kaes correlates this difference in cortical structure with the fact that taste and smell which have their center in the gyrus fornicatus, are used less by Europeans than by Asiatics, and are less differentiated. The abnormal brains, the twenty-five year dwarf and the microcephalic child each had a cortex in an incomplete stage of medullation. That of the dwarf was little beyond that of the 1 $\frac{1}{4}$ year child.⁴ That of the microcephalic child was still less developed than that of the child.⁵ Both the abnormal brains are to be regarded as cases of inhibition in the growth process.

The foregoing account pretends to be but a bare outline of the most important of Kaes' results, presented as far as possi-

¹ 6, pp. 14-15.

² 6, p. 10.

³ 6, p. 12-13.

⁴ 11, p. 5, p. 9.

⁵ 11, p. 9.

from Kaes' own standpoint. No attempt has been made to do justice to the mass of details contained in the papers, nor has there been any pretense to criticism of method or results, except where apparent contradictions within Kaes' own account occur. It is obvious that there is a wide **discrepancy** between Kaes' measurements of cortical thickness and those of other observers, a discrepancy which cannot be readily explained. Until this difference is explained, it is impossible to accept Kaes' results unquestioningly. The whole problem of cortical thickness at various ages, and its significance is evidently in need of further investigation.

LIST OF KAES' PAPERS—IN CHRONOLOGICAL ORDER.

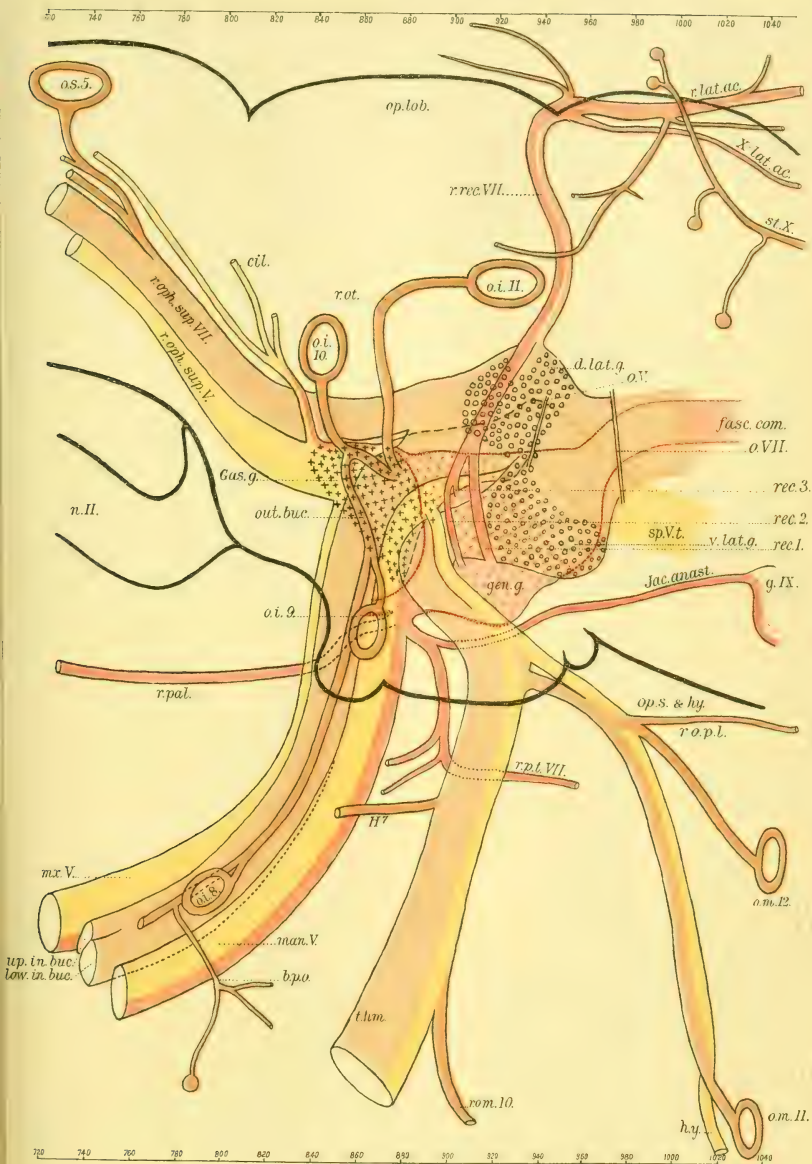
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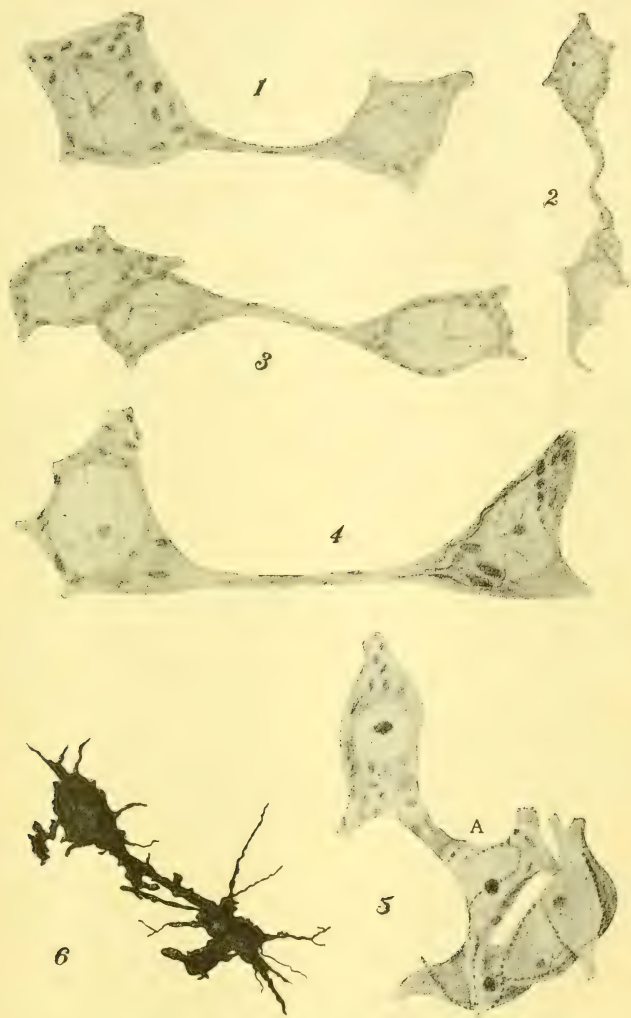
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THE GIANT GANGLION CELLS OF CATOSTOMUS
AND COREGONUS.

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With Plates XXIV and XXV.

The giant cells in the spinal cord of fishes have presented great difficulty to impregnation by the Golgi method. I do not know of any description of these cells based on Golgi preparations, and Sargent ('98) states that he tried the Golgi and methylene blue methods exhaustively without results. The following description is based upon very satisfactory preparations by the Golgi method of the nervous system of embryos of *Catostomus sp.* and *Coregonus albus*, under 2 cm. in length.

I shall describe first the cells and their processes in *Catostomus* and then note briefly their special characters in *Coregonus*. In sections treated with the Ehrlich-Biondi triple stain these cells stand out clearly on account of their large bodies which are colored red in contrast to the smaller cells whose large nuclei are stained green. In a horizontal section of an entire embryo, which fortunately includes the whole length of the spinal cord, 105 of these large cells are to be counted. These preparations show nothing concerning the processes of the cells, but their position is clearly made out. They lie close to the dorsal surface of the cord (frontal or sagittal sections), and at either side of the middle line. Compare Figs. 2 and 3. The bodies of the cells may touch or cross the median plane, but the larger part of every cell lies to one side. At the cephalic end of the cord the cells are found in close proximity to the commissura infima Halleri, which I have described in a paper on the brain of *Acipenser*, now in press. In a few cases I have found one or two

cells at the sides of this commissure, lying apparently in the course of the spinal V tract in the medulla. Caudally the cells continue nearly to the end of the cord.

I have twenty-one series of Golgi sections in the three planes which show these cells, and in eleven series of longitudinal sections many cells are impregnated in all segments of the cord and also in the medulla in the position indicated above.

The cell bodies are rounded, pear-shaped, or cuboidal and are about equal in size to the spinal ganglion cells in the same sections. There is always a single dendrite arising from the caudal or lateral end of the cell. In some cases the dendrite is slender near the cell (Figs. 4 and 7), while in the majority of cases it is thick throughout its whole extent. The dendrite runs caudally from the cell for a variable distance (compare cells shown in Fig. 2), near the dorsal surface of the cord and between the median line and the dorsal tracts (Figs. 5 and 6). It then bends dorsally or dorso-laterally and emerges from the cord. At this point the dendrite thickens greatly, if it is slender in its earlier course. As it rises toward the dorsal surface of the body the dendrite is often sinuous and very commonly makes loops in its course (Fig. 2, *A*, *C*, and Fig. 7). Frequently it retains its thickness until it reaches the surface, where it ends with a small knob apparently just beneath the epidermis. There may be branches in these cases which have not been impregnated. In many cases, at least, one or two branches are found and in a few cases the terminal branching appears to be well developed (Figs. 2, 4, 5). All the cells which have been impregnated have dendrites of the above description, and in many cases the dendrites have been impregnated without the cell body taking the stain.

Each cell has two neurites, although occasionally only one neurite appears in the section, possibly owing to incomplete impregnation. In rare cases a single neurite divides in T-form. Of the two neurites, one is directed rostrally, the other caudally. The rostral neurite arises from the cell body, soon turns laterally and joins the dorsal tract of its side. Some fibers of the dorsal tracts are always impreg-

nated in these preparations and the tracts can usually be identified with perfect certainty in any given preparation by means of the central processes of the spinal ganglion cells (Figs. 4, 5, 6, 7). The rostral neurites are slightly coarser than the fibers of the dorsal tracts, sometimes much coarser. They can be traced forward for a considerable distance in most preparations before being lost among the dorsal tract fibers. In a few cases I have traced these fibers with certainty to the cephalic end of the cord (Fig. 3) and in one case (Fig. 2 *A*) have found the fiber breaking up into a number of branches in the nucleus funiculi. In the same individual two cells situated in the caudal part of the medulla send their neurites forward in the spinal V tract toward the tuberculum acusticum. The latter body is identified by the entrance and end-branching of the fibers of the lateral line VII nerve (Fig. 2 *A*). In many cases the rostral neurites bear small lateral twigs and longer branches similar to those seen on the fibers of the dorsal tracts.

The caudally directed neurite arises usually from some part of the dendrite, occasionally from the cell body, and rarely by T-division of a single neurite (Fig. 6 *B*). It also runs among the fibers of the dorsal tracts. The fiber is more slender than either the rostral neurite or the fibers of the dorsal tracts. It frequently shows divisions early in its course (Fig. 2) and is not so long as the rostral neurite.

There are a few exceptional cases in which the dendrites go to the opposite side of the body from that on which the cell lies, but the neurites never cross to the opposite side.

In *Coregonus albus* the number of cells is very much less than in *Catostomus*, but my histological sections are not satisfactory for counting the entire number in any one specimen. The number is probably between forty and fifty. The only other difference between these elements in *Coregonus* and *Catostomus* lies in the fact that in *Coregonus* the dendrite is directed rostrally and the rostral neurite arises from the dendrite, while the caudal neurite arises from the cell body or from the dendrite (Figs. 8, 9).

The interpretation of these cells seems to be not difficult.

Their neurites correspond closely to the central processes of the spinal ganglion cells. This correspondence is complete in those rare cases in which there is a single neurite dividing into rostral and caudal (ascending and descending) branches. Their dendrites also may be compared with the peripheral processes of the spinal ganglion cells, being distributed to the integument. The comparison is striking in the case of spinal ganglion cells such as those shown in Figs. 4 and 7, which send their peripheral processes up to the dorsal surface. The existence of cells within the spinal cord which correspond in function and in the disposition of their processes to the spinal ganglion cells may be explained by the hypothesis that they are derived ontogenetically from the neural crest, from which the spinal ganglia arise, but have failed to migrate with those ganglia. The distribution of the dendrites of these belated cells suggests that they may be compared most closely with the cells whose peripheral processes go into the dorsal rami of the spinal nerves.

Comparative anatomical investigations seem to show that in the phylogeny of vertebrates the spinal ganglion cells have been derived from the spinal cord. In *Amphioxus* (Retzius '90) the sensory roots of the spinal nerves, which are without ganglia, arise from cells within the spinal cord. Retzius describes three varieties of such cells: transverseiy disposed bipolar cells, one of whose processes divides into a peripheral fiber and a fiber of the longitudinal tract, while the other process goes to the longitudinal tract of the opposite side; multipolar cells; and longitudinally disposed bipolar cells sending one process into the sensory root and the other into the longitudinal tract of the same side. Retzius points out that *Amphioxus* is the only vertebrate whose dorsal roots have no ganglia but arise from cells within the cord. Kölliker ('96, p. 158) suggests that the cells which give rise to the sensory nerves in *Amphioxus* are homologous with the neural crest of the embryos of higher vertebrates, and that this crest is therefore to be considered as derived from the cord rather than as a direct derivative of the ectoderm.

In *Petromyzon* Freud ('78) found longitudinally disposed

bipolar cells in the dorso-median part of the cord which send their nervous processes into the sensory roots. These cells correspond (Kölliker) to the above mentioned cells in *Amphioxus*, and *Petromyzon* presents an intermediate condition between *Amphioxus* and the higher vertebrates. The presence of these cells in *Petromyzon* also lends support to Kölliker's hypothesis regarding the neural crest.

In *Pristiurus* embryos, according to Lenhossék's researches ('92), some fibers pass through the spinal ganglia without connection with ganglion cells. It is possible that these arise from cells within the cord, corresponding to those in *Petromyzon*.

Tagliani ('98) states that in *Solea impar* and *Orthogoriscus mola* the greater part of the giant cells send their fibers caudad in a bundle from which occasional fibers go toward the sensory roots among the fibers of which they are lost. He thinks that in these two forms, as also probably in *Lophius piscatorius*, a part but not all of the fibers of the giant cells enter the dorsal roots. A few fibers from the giant cells run rostrad in a bundle which is lost on the floor of the medulla lateral to the fasciculus longitudinalis posterior. He concludes: "dass die Nervenfortsätze der Riesennervenzellen sich nicht im Fasergewirr der spinalen und bulbären Centren auflösen, sondern als nackte Nervenfasern zu centrifugalen (motorischen) Elementen der dorsalen, spinalen, oder bulbären Wurzeln werden."

From these investigations it appears that in *Amphioxus*, *Cyclostomes*, *Selachians* (?), and *Teleosts* cells are present in the spinal cord which give rise to fibers of the dorsal roots of the spinal nerves. In *Amphioxus* and *Petromyzon* these fibers are certainly afferent (sensory) and it is to be presumed that the same is true in *Selachians* and *Teleosts*. The disposition of the processes of these cells within the cord is known only in *Amphioxus*, where they correspond in a general way to the central processes of the spinal ganglion cells in higher vertebrates. The cells described in the present paper have peripheral processes distributed to the integument and central processes (neurites) running in the dorsal tracts and ending in the dorsal horns and the nucleus funiculi. This justifies the con-

clusion that the giant ganglion cells in the spinal cord of at least some Teleosts are directly homologous with the cells in the cord of *Amphioxus* which give rise to the fibers of the sensory roots. I have made no investigations to determine whether these cells are present in adult specimens of *Catostomus* or *Coregonus*, but they seem to be less numerous in the older embryos investigated and they may disappear in the adults. If so, their vestigial character would perhaps account for the fact that their peripheral processes do not enter the dorsal roots of the spinal nerves, but make their exit nearer the mid-dorsal line.

It is impossible at present to make any direct comparison of the cells here described with the giant ganglion cells in other fishes, except those described by Tagliani (see above). I shall therefore omit any further review of the literature of giant cells, although giving a list of the papers consulted. The study of the processes of the cells by previous authors has been necessarily incomplete on account of the methods employed. Further investigations by the Golgi and methylene blue methods will be necessary before any safe conclusions as to homologies can be reached.

Morgantown, W. Va., Sept. 3, 1900.

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DESCRIPTION OF FIGURES.

ABBREVIATIONS.

- a.*—auditory sac.
ac.—tuberculum acusticum.
c.—central process of spinal ganglion cell.
ch.—notochord.
d.—dendrites.
e.—epithelial cells.
f.—dorsal tracts of cord.
g.—giant cells.
m.—body muscles.
med.—medulla.
n. n'.—rostral and caudal neurites, respectively.
p.—peripheral process of spinal ganglion cell.
sp. c.—spinal cord.
sp. g.—spinal ganglion cell.
N. l. l.—lateral line VII nerve.

An arrow indicates the cephalic direction in each drawing.

PLATE XXIV.

Fig. 1. Horizontal section of part of medulla and spinal cord of *Catostomus* embryo 10 days after fertilization.

Fig. 2. Sagittal section of the medulla and cord of a 12-day *Catostomus* embryo, showing twenty giant cells and several dendrites whose cells are not impregnated. The segments *A*, *B*, and *C* are successive and continuous.

Fig. 3. Horizontal section of the cephalic part of the cord of a 12-day *Catostomus* embryo.

Fig. 4. Sagittal section of part of the cord of an 18-day *Catostomus* embryo. Camera drawing.

Fig. 5. Horizontal section of part of the cord of a 19-day *Catostomus* embryo.

PLATE XXV.

Fig. 6. Horizontal section of the cephalic half of the cord of a 19-day *Catostomus* embryo. *B* continues immediately after *A*.

Fig. 7. Sagittal section of part of the cord of a 26-day *Catostomus* embryo. Camera drawing.

Fig. 8. Horizontal section of part of the cord of a *Coregonus* embryo shortly after hatching.

Fig. 9. Sagittal section of a part of the medulla and cord of a *Coregonus* embryo shortly after hatching. The cell marked thus (?) probably is not connected with the dendrite with which it appears to be in connection, but underlies it.

ARRANGEMENT AND TERMINATIONS OF NERVES IN THE ŒSOPHAGUS OF MAMMALIA.

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With Plate XXVI.

Since but little work has been done on the innervation of the œsophagus, it seemed to me that it might be both interesting and profitable to determine, by means of the *intra-vitam* methylene blue method, the arrangement and terminations of the nerves in this part of the digestive tract, to verify the results already gained by other methods and, so far as practicable, to compare the innervation of the œsophagus with that of other parts of the alimentary canal.

In pursuance of these purposes, I have confined my investigations to the œsophagus of the cat and rabbit and have used only the *intra-vitam* methylene blue method. In most cases, I injected into the thoracic aorta, proximal to the arch, a 1% solution of methylene blue in normal salt solution, the quantity varying with the size of the animal and the special purpose to be attained. When necessary, the carotids at the level of the thyroid cartilage and the aorta just above the diaphragm were ligated before the injection was made. After a time varying according to whether the staining of the motor or of the sensory apparatus was especially desired, the œsophagus was removed and the mucosa with the muscularis mucosæ and the submucosa was separated from the underlying muscular coats. When the nerves seemed sufficiently stained, the tissue was fixed, either in a saturated solution of ammonium picrate, as recommended by Dogiel (9), or, after fixation for a few minutes in the ammonium picrate solution, was removed to the 10% solution of

ammonium molybdate (Bethe (3)), in which it was allowed to remain for about twelve hours. The tissues fixed by the former method were cleared and mounted in equal parts of glycerine and the ammonium picrate solution; those fixed by the latter method were washed, dehydrated, cleared in xylol and either mounted at once in balsam or embedded in paraffin and sectioned, some transversely to the surface and others tangentially. The second method of fixation was used especially to avoid the maceration of the epithelium, which, after the continued action of the ammonium picrate, was often so excessive as to leave but little epithelium and hence but few of the terminations of the nerves in the epithelium.

Arrangements and Terminations of the Nerves in the muscular coats. Between the circular and longitudinal muscular layers, the nerve trunks, which, after ramifying in the outer connective tissue sheath, have penetrated the longitudinal muscular layer, form a coarse meshed plexus, at the nodal points of which numerous nerve cells forming larger or smaller ganglia are found. In the œsophagus of the rabbit and in the upper part of the œsophagus of the cat, where striated muscle constitutes the muscular coats, the ganglia are much smaller and less frequent and contain relatively few nerve cells. The nerve cells comprising these ganglia vary in size and shape. Most of them are multipolar cells, each having a round or oval nucleus, a distinct nucleolus, a granular and pigmented protoplasm, with many dendritic processes and one neuraxis. The dendritic processes are usually short and thick and break up into a large number of branches which extend between the cells of the ganglion, forming a more or less intricate network, in the meshes of which the nerve cells are sometimes enclosed. In the latter case, we have an appearance like the "nidos pericellulares" described by Ramón y Cajal (4-7) for the ganglia of Auerbach's plexus of the intestinal canal, which Dogiel (11) has shown to be the result of an accidental enclosure of the cell, to be always extra-capsular, and of less physiologic importance than was assigned to them by Cajal. Occasionally, as described by Dogiel for the cells of the ganglia of Auerbach's plexus of the intes-

tine, one of the dendrites of these cells may be longer than the others and even extend through a nerve trunk to another ganglion. The neuraxis of this kind of cell is long and extends out into one of the nerve trunks leading from the ganglion, usually as a non-medullated (Remak's) fiber; it may often be traced, with no or very little branching, till it leaves the nerve trunk and enters into the formation of the intra-muscular plexuses, surrounding and supplying the non-striated muscles of the muscular coat and to some extent also of the muscularis mucosæ. Although it has been shown by Kölliker (27 and 28), Dogiel (10) and others that the neuraxes of sympathetic neurones may possess a thin medullary sheath, it has seemed to me that most, at least, of the neuraxes of the neurones whose cell bodies constitute the ganglia of the intermuscular plexus of the œsophagus, were non-medullated throughout their course. This observation corroborates one made by Huber (20), who says that he believes that the neuraxes of the cells of the peripheral ganglia,—those of the heart, salivary glands, intestine, bladder, etc.—are non-medullated throughout. The endings of these neuraxes are as described for the nerve endings in non-striated muscle of other parts of the body, the terminal branch dividing into two or three short twigs which end in an enlargement *on* the non-striated muscle cell (Huber and DeWitt (26)). While the arrangement of the muscular plexus is usually so complicated that it is impossible to trace a single neuraxis from the cell body where it originates to its termination on a muscle cell, yet I have occasionally seen a fiber which had a shorter course. In these cases, the fiber could, without difficulty, be traced from the cell body, leaving the ganglion, often without forming part of a nerve trunk, but passing independently to a muscle fiber in the vicinity of the ganglion. While most of the neuraxes of the sympathetic cells of the intermuscular plexus of the œsophagus end on the non-striated muscle cells of the muscular walls of the œsophagus, I have at times, as I believed, been able to trace certain neuraxes to the walls of the blood vessels, where they helped to form the vascular plexus of vaso-motor nerves. As this observation, however,

was made only in surface preparations, where it is possible to mistake a fiber passing over or under a vessel for one ending upon it, I am unwilling to make this statement positively until after further investigation.

Besides the neurones which have just been described and which may be regarded as motor sympathetic neurones both on account of their resemblance to the cells described as motor neurones in other sympathetic ganglia by Dogiel (10-12), Huber (20-21) and others, and from the fact that their neuraxes have been traced to their terminations on non-striated muscle cells, we find other cells in the ganglia of the œsophageal intermuscular plexus. These are usually spindle-shaped, with round or oval nucleus and granular protoplasm; from each extremity extends a single slender process, difficult to differentiate into neuraxis and dendrite and both forming parts of nerve trunks. The cells may be multipolar, with one neuraxis and several long slender dendritic processes, many of which extend into the nerve trunks leading from the ganglion. These cells stain more readily in methylene blue than do the motor cells; they are often situated near the periphery of the ganglion and are sometimes found embedded in a nerve trunk at some distance from any ganglion. While the processes of these cells enter the nerve trunks and may often be traced for some distance in them, I have never been able to trace them to their termination. They, however, correspond exactly to the cells described by Dogiel (12) as type II or sensory cells and found by him in both the central and peripheral sympathetic ganglia. According to Dogiel, the single neuraxis of one of these cells passes in the nerve trunk, either as a non-medullated fiber or surrounded by a thin medullary sheath, to some other ganglion in which it forms an intercellular network. It often sends collateral branches to several ganglia, before finally terminating as described about the motor sympathetic cells. Huber (20), having seen sympathetic fibers terminating on the dendrites of sympathetic cells, suggests the possibility that this is the manner of termination of the neuraxes of the sensory sympathetic neurones. Other neuraxes of sensory sympathetic neurones,

or their collaterals, according to Dogiel, pass through the rami communicantes, to the spinal ganglia and end, as described by Aronson (1) and Cajal (7) in pericellular plexuses about the spinal ganglion cells. The dendrites of these type II cells are described as long, slender and branching, difficult to distinguish from neuraxes and, according to Dogiel (12), they may be traced, either through the nerve trunks or in an independent course through the circular muscular coat, into the submucosa and mucosa. He, basing his assumption on the work of Sakus-sef (37), who believed he could trace these dendrites, in the intestine of the fish, through a subepithelial plexus into the epithelium, says: "Es ist möglich dass die Endverzweigungen dieser Fortsätze in den inneren Organen ebensolche sensible Apparate bilden, wie die sensiblen Fasern des Cerebro-spinal-systems in der Haut, etc." This would, if verified, form a complete apparatus for peripheral sympathetic reflexes.

In the periphery of these ganglia and along the nerve trunks, as well as in the mucosa and submucosa, are seen many branched cells, with long, slender, nerve like processes, which stain readily in methylene blue and in some respects resemble nerve cells. These seem to correspond to the cells described by Ramón y Cajal (4, 5) as nerve cells, which Dogiel (11) has demonstrated in the adventitia of arteries, in the sheaths of nerves and ganglia and in the connective tissue between the bundles of smooth muscle fibers. While their processes often resemble the processes of nerve cells and may even seem at times to be in communication with nerve fibers, these seem to be cells of connective tissue origin rather than nerve cells.

Many of the cell bodies of the sympathetic neurones of type I of the intermuscular plexus of the œsophagus are surrounded by pericellular end-baskets, the telodendria of small medullated fibers, found in the nerve trunks and sending collateral branches to several ganglia before finally terminating. In any ganglion, one or two or three of these fine fibers may be seen, which often lose their medullary sheaths some time before terminating; they often branch several times in the ganglion, so that a single fiber may influence, through its collateral

branches, several cells in a single ganglion, as well as several ganglia. At its termination, each terminal branch breaks up into varicose twigs, which surround the type I cells in an end-basket which has been shown to be within the capsule of the cell. Similar end-baskets have been found, surrounding sympathetic cells in both central and peripheral ganglia in all parts of the body. As shown by Dogiel, Huber and others, they are the telodendria of white rami fibers or preganglionic fibers and are always intra-capsular. While these pericellular baskets have been found by Huber (21) in the ganglia of the œsophagus as well as in those of the intestine, he states that he believes that not all the cells of these ganglia are thus connected to the cerebro-spinal system, since the number of baskets found has been relatively small.

The question of the character of the ganglia of Auerbach's plexus in the intestine has been discussed by Langley and Anderson (33), Kölliker, Huber, and others and, in spite of the apparent failure of Langley's physiologic experiments, the conclusion seems indisputable that these ganglia, as well as the ganglia of the œsophagus which are analogous to them, are sympathetic, since they correspond histologically in every respect to other sympathetic ganglia and like them are connected to the cerebro-spinal system by white rami fibers which terminate in pericellular, intracapsular end-baskets about the cells of the ganglia.

The nerve trunks of the intermuscular plexus of the œsophagus contain the white rami or preganglionic fibers, the non-medullated neuraxes of the sympathetic motor cells and the neuraxes and dendrites of the sympathetic sensory cells already mentioned; in addition to these, they contain non-medullated nerves, the neuraxes of sympathetic cells, whose cell bodies are situated either in the ganglia of the œsophagus or in more distant ganglia, the fibers forming a perivascular plexus and terminating on the smooth muscle fibers of the vessel walls; besides these, we find larger medullated nerves, which pass through the ganglia without making connection with any of the cells and pass into the submucosa and mucosa to end as will be

described later. Such large medullated nerves have been found in all parts of the sympathetic system and are generally recognized as cerebro-spinal sensory fibers. Kölliker (28) says that the sensory fibers of the sympathetic system are larger or smaller medullated fibers originating from the spinal ganglia and conveying the scanty sensory impressions which emanate from the several organs. In the upper and middle thirds of the œsophagus of the cat and in the whole œsophagus of the dog and rabbit and other animals which have striated muscle in the muscular coat throughout the whole œsophagus, other medullated nerves are found in the nerve trunks, which form no connection with the sympathetic ganglion cells, but, sooner or later, leave the nerve trunk to terminate on the striated muscle in an end-plate which is exactly like the end-plate found in voluntary muscle in all parts of the body.

The origin of these various nerves has been investigated by Howell and Huber (22), Langley (31), Kronecker and Lüscher (29), Kreidel (30) and others. Howell and Huber, while investigating the physiology of the communicating branch between the superior and inferior laryngeal nerves, determined that this was a sensory branch of the superior laryngeal nerve and carried sensory fibers from the trachea and œsophagus. Kronecker and Lüscher decided, as the result of their experiments, that the inferior or recurrent laryngeal nerve brought the motor fibers to the cervical and upper thoracic portions of the œsophagus. Langley found that the motor innervation of the whole œsophagus and of the cardiac end of the stomach is from the vagus nerves, which also carry inhibitory fibers to the cardiac and adjacent regions of the œsophagus. Kreidel, however, has carried out a number of experiments to determine from which root arise the nerves supplying the œsophagus and decided that, while the vagus nerves carry the fibers to their place of distribution, they arise, not from the vagus root, but from the glossopharyngeal. By comparing the results of these workers, we may arrive at the conclusion that all the nerve fibers—motor, sensory, vaso-motor and preganglionic—found in the nerve trunks of the intermuscular plexus of the œsoph-

agus, except the neuraxes and dendrites of the nerve cells found in the œsophageal ganglia, arise from the vagus nerves.

Pl. XXVI, Fig. 1 represents, drawn under low magnification, a surface view of a portion of the intermuscular plexus of the lower part of the œsophagus of a cat. In it we get a general view of the plexus and ganglia and, to some extent, see the two kinds of nerve cells and various kinds of nerve fibers constituting the nerve trunks. This, however, is better shown in Pl. XXVI, Fig. 2, *A*, which represents a portion of the same figure drawn under higher magnification. In this figure, the motor and sensory cells are plainly distinguished, with their neuraxes and dendrites extending out into the nerve trunks or breaking up in the ganglion. Other non-medullated fibers may be seen passing through the ganglion, the neuraxes of cells of some other ganglion on the way to their destination. Two large medullated fibers pass through the ganglion without making connection with any of its cells; these are sensory fibers, the dendrites of spinal ganglion cells. We may also distinguish two smaller medullated fibers, which lose their medullary sheaths near the center of the ganglion and send non-medullated fibers to several cells, about which they form pericellular networks. This relation of the white rami fibers to the ganglion and the formation of the end-baskets may be better seen, however, in *B* of the same figure, which represents a surface preparation of a ganglion from the intermuscular plexus of a rabbit, in which the cells with their processes were very imperfectly stained, but the white rami fibers with their telodendria were very clearly brought out. Occasionally in this preparation, only the peripheral zone of the cell is stained, the central part and nucleus and the processes being completely unstained.

Arrangement and terminations of Nerves in the Submucosa and Mucosa. In the submucosa of the œsophagus, smaller nerve trunks form a finer meshed plexus analogous to Meissner's plexus of the stomach and intestine. These nerve trunks contain medullated and non-medullated nerves, many of them originating from the intermuscular plexus. Few ganglia have been found by me, however, in this submucous plexus of the

oesophagus. In the course of the nerve trunks and occasionally at the nodal points of the plexus, single usually bipolar, but occasionally multipolar nerve cells are found, which, according to Dogiel's (12) definition, are sensory sympathetic cells. In the lower part of the oesophagus, I have occasionally seen small ganglia containing from four to eight cells, some of which were surrounded by the telodendria of white rami fibers. These ganglia, when present, show the two types of nerve cells with their processes found in the ganglia of the intermuscular plexus; they present also the large medullated sensory fibers and fine non-medullated sympathetic fibers passing through the ganglion on the way to their termination. Such a ganglion is represented in Pl. XXVI, Fig. 4. This ganglion was found in the lower part of the oesophagus of a cat and presents four large cells, of which one is surrounded by the end-basket of white rami fibers, the others showing the long, fine, dendritic processes characteristic of sensory cells. The form of plexus found in the greater part of the oesophagus is represented in Pl. XXVI, Fig. 3, showing the interwoven nerve trunks with here and there a few, isolated cells. While I have never been able to trace a fiber of the submucous plexus from its origin in a cell to its termination, it has seemed to me probable that most, if not all, of the type I cells found in this plexus are secretory cells, whose neuraxes terminate on the gland cells. Typical oesophageal glands are found in the submucosa only in that part of the oesophagus in which ganglia are seen. Both medullated and non-medullated fibers follow the course of the gland ducts, the former terminating, as in the salivary glands (Arnstein (2) and Huber (23)), in free endings on the epithelial cells of the duct, while the latter form a plexus about the acinus, from which branches may be traced to their endings in slight enlargements on the gland cells. I have found no ganglion cells in direct connection with any of these glands.

The blood vessels of the submucosa, as well as those of other parts of the oesophagus, are, like the vessels of other parts of the body (Dogiel (13), Schemetkin (38) and Huber (24)) supplied with medullated sensory fibers, which end in telodendria

in and around the adventitia, and non-medullated sympathetic, vaso-motor fibers, which form a plexus in the adventitia and end on the non-striped muscle of the media.

Non-medullated nerves, the neuraxes of neurones, the cell bodies of which are found in the ganglia of the intermuscular plexus of the Œsophagus, pass through the nerve trunks of that plexus, penetrate the circular muscular layer, help to form the nerve trunks of Meissner's plexus and finally, leaving this plexus, break up into an intra-muscular plexus in the muscularis mucosæ, from which fine fibers are given off which end on the muscle cells as on non-striped muscle in other parts of the body. The general arrangement of this intra-muscular plexus and its relation to the submucous plexus is shown in Pl. XXVI, Fig. 3, which represents, sketched under low magnification, a portion of the muscularis mucosæ with the submucosa over it.

The large, medullated, sensory fibers, found in the nerve trunks of both the intermuscular and the submucous plexus, pass through the muscularis mucosæ and form, with frequent branching, a finer meshed plexus in the deeper parts of the mucosa. From this plexus branches, still medullated, are given off, which pass, repeatedly dividing at the nodes of Ranvier, toward the epithelium. Under the epithelium, these nerve fibers lose their medullary sheaths and form a fine meshed sub-epithelial plexus, whose fibers extend for considerable distances under the epithelium. Before losing their medullary sheaths, many of the medullated fibers give off at the nodes of Ranvier non-medullated fibers, which also pass up toward the epithelium and assist in the formation of the sub-epithelial plexus. From this plexus, as well as from non-medullated fibers which come up directly from the mucosa and seem to take no part in the formation of the plexus, fine, varicose nerves pass up into the epithelium, wind between the epithelial cells, occasionally giving off longer or shorter branches, which terminate in varicosities of different forms and sizes; the terminal fibers also finally end in ball-like thickenings on or between the epithelial cells, either near the surface or at a greater depth.

A well stained preparation of the Œsophageal mucosa,

viewed from the surface, presents an intermingled and confused mass of nerves, medullated and non-medullated, with their telodendria, in which it is impossible to trace any single fiber through all its branchings to its terminations and so view in a connected and orderly way the relations of the several parts to each other. Occasionally however, a preparation may be obtained in which, in a given area, few or perhaps only one fiber is stained with the methylene blue and this one very perfectly to its minutest branches. In this case, we may observe over how large an area a single nerve is distributed. Pl. XXVI, Fig. 5, represents such a fiber with its terminal branching. As this is taken from a rather thick, tangential or somewhat oblique *section* of the mucosa, however, and not from a surface preparation, there is no doubt that many of the terminal branches with their telodendria have been removed and that the ending, if complete, would occupy a much larger area. This has been demonstrated in surface preparations, in some of which the medullated and non-medullated nerves have been traced through much more complicated branching and dividing than that shown in the figure. The end-branches of these nerves intertwine and overlap in such a way that a surface view of the mucosa with the surface of the epithelium in focus shows an almost uniform distribution of the telodendria in most of the epithelium.

When we compare the small number of the large, medullated, sensory fibers found in the nerve trunks of the œsophageal plexuses with the large number of non-medullated nerves taking part in the free sensory ending in the epithelium, we are convinced that each nerve divides repeatedly and covers with its branches a relatively large area. Similar free sensory nerve endings have been found in the ducts of the salivary glands by Arnstein (2) and Huber (23), in the respiratory tract by Plosschko (35), Berkley (2a) and Smirnow (39), in the endo- and peri-cardium by Smirnow (40) and Dogiel (13) and in the bladder by Ehrlich (16), Cuccatti (8), Grünstein (19) and Huber (24). The latter has described and figured, from the mucosa of the urethra of a cat, a free sensory ending in which twenty medullated nerve fibers arising from a single nerve fiber could

be counted, each giving off numerous non-medullated branches with their divisions and telodendria; the whole ending was estimated to cover an area 1.4 mm. by 0.8 mm. As Gaskell (17), Edgeworth (15) and Langley (32) agree that the number of sensory fibers in the white rami is small, Huber believes that "this may be compensated for by the repeated division of those fibers and by the relatively large area covered by their branches." Both the terminal branches after losing their medullary sheaths and the collateral non-medullated branches given off from the medullated fibers at some node of Ranvier are beset with varicosities of different forms and sizes.

That the terminal and lateral arborizations surround the epithelial cells, ending on or between the cells in small varicose thickenings, sometimes on the surface cells and sometimes on the deeper ones, may be seen in Pl. XXVI, Fig. 7, taken from a cross section of the œsophageal mucosa of a young cat. In the greater part of the œsophagus, these terminal arborizations seem to be quite evenly distributed and it has seemed to me probable that nearly all of the epithelial cells come in contact with one or more of the terminal nerve fibers. In the upper part of the œsophagus, however, near its junction with the pharynx, there are, in addition to these uniformly distributed telodendria, certain peculiar ball-like masses, consisting of the telodendria of several nerve fibers, whose branches are very short and soon become non-medullated. The non-medullated fibers soon break up into long, slender, varicose end-branches, forming end-brushes which meet and intermingle with the end-brushes of other nerve fibers, making a dense and compact mass of terminal nerve fibers, which, on superficial examination, resembles a special sensory end-organ. Closer study, however, fails to reveal the presence of a connective tissue capsule and, in cross sections, we find that the ending is in the epithelium and does not differ from the end-arborizations in other parts of the mucosa except for the fact that here they are more closely crowded together, more richly branched and beset with larger and more abundant varicosities. Pl. XXVI, Fig. 6, represents the surface view of one of these end-balls, which I have found

only in the pharyngo-œsophageal region, but which I have found there in considerable numbers. Two large medullated nerves are seen, which divide repeatedly into short medullated branches, these breaking up almost at once into terminal end-brushes, whose extremities meet and intermingle with those from the fiber at the opposite extremity of the mass of telodendria. Fig. 8 represents a cross section of a similar mass of endings, showing the fine sub-epithelial plexus and the rich branching of the terminal varicose fibers in the epithelium.

The nerves ending in the mucosa of the frog's œsophagus have been stained in gold chloride by Goniaew (18), working under Arnstein's direction, and in chrome silver by Smirnow (41). Both describe the formation of plexuses of medullated fibers in the deeper parts of the mucosa and of non-medullated fibers just under the epithelium, from which varicose fibers were traced into the epithelium. The nerve fibers in the epithelium, according to Smirnow, run either straight or in a more or less winding course, between the epithelial cells, divide several times, and, as fine, varicose fibers, surround the ciliated, as well as the goblet cells which line the œsophageal mucosa of the frog, ending free on both kinds of cells, either in points or in knob-like thickenings. The goblet cells have an especially rich nerve supply and are here regarded as unicellular glands.

Malischeff (34) has recently investigated the nerve endings in the œsophagus of the bird, but I have not had access to his report of the results of his investigations.

Retzius (36), with the chrome silver method, demonstrated nerves entering the epithelium of the œsophageal mucosa of the cat. These nerves branched freely in the epithelium and ended between the epithelial cells. He says, however, that the nerves in the œsophageal mucosa are by no means so numerous as in that of the pharynx and larynx and end much nearer the basement membrane. While some of the terminal fibers in my preparations end on the deeper cells of the epithelial layer, many may be traced, as seen in Pl. XXVI, Fig. 7, to the flattened cells near the surface, on which they may be seen to end.

In summarizing the results of my investigations, it may be

said that the œsophagus receives its motor and secretory innervation through sympathetic neurones the cell bodies of which are situated in the ganglia in the intermuscular (Auerbach's) and the submucous (Meissner's) plexuses, the neuraxes of which terminate on the non-striped muscle of the muscular coat and of the muscularis mucosæ and on the gland cells of the submucosa in those portions of the œsophagus in which glands are found. These sympathetic neurones are, in part at least, connected to the cerebro-spinal system by white rami or preganglionic fibers, which terminate in intracapsular end-baskets surrounding the cell bodies. In so far as the muscular wall of the œsophagus consists of striated muscle, it receives its motor innervation through medullated fibers, the neuraxes of motor neurones, the cell bodies of which are situated in the anterior horn of the spinal cord, and which terminate in motor end-plates as in voluntary, striated muscle in other parts of the body. The œsophagus receives its sensory innervation through the dendrites of spinal ganglion cells which terminate in free sensory endings in the adventitia of the blood vessel walls and in the epithelial lining of the mucosa and of the gland ducts. There are in addition sympathetic neurones, the cell bodies of which are situated in the ganglia of the œsophageal plexuses and along their nerve trunks, the neuraxes of which are believed to terminate in other sympathetic ganglia or in the spinal ganglia, while the mode of termination of the dendrites has not yet been determined; these are the so-called sensory sympathetic neurones which may be concerned in the establishment of peripheral sympathetic reflexes.

I desire to acknowledge my indebtedness and to express my sincere gratitude to Professor Huber for many valuable suggestions and for other help rendered in the prosecution of this work.

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DESCRIPTION OF FIGURES.

PLATE XXVI.

Fig. 1. Surface preparation of part of the intermuscular plexus of the œsophagus of a young cat. Stained in methylene blue and fixed in ammonium picrate. Sketched with the aid of the camera lucida under $\frac{2}{3}$ in. objective and 2 in. ocular. Reduced to $\frac{1}{3}$.

Fig. 2, A. Surface preparation of one of the ganglia from *Fig. 1*. Sketched under $\frac{1}{6}$ in. objective and 2 in. ocular with the aid of the camera lucida. Reduced to $\frac{1}{3}$. *a.*—sympathetic fiber passing through ganglion; *s.s.*—sensory cerebro-spinal fibers passing through ganglion; *m.m.*—sensory sympathetic cells; *c.c.c.*—motor sympathetic cells surrounded by end-baskets of white rami fibers; *p.*—preganglionic fiber.

Fig. 2, B. Surface preparation of ganglion from intermuscular plexus of rabbit. Stained in methylene blue, fixed in ammonium picrate. Cells imperfectly stained, but end-baskets of preganglionic fibers showing very distinctly. Drawn with the aid of the camera lucida, under $\frac{1}{6}$ in. objective and 2 in. eye-piece. Lettering same as in *A*.

Fig. 3. Surface preparation of submucosa and muscularis mucosæ of young cat. Stained in methylene blue and fixed in ammonium picrate. Drawn with the aid of the camera lucida, under $\frac{2}{3}$ in. objective, 2 in. eye-piece. Reduced to $\frac{1}{3}$. *p*—intramuscular plexus; *s.s.s.*—sensory sympathetic nerve cells; *t.*—nerve trunk of submucous plexus; no type I cells are seen in this part of the plexus.

Fig. 4. Surface preparation of small ganglion from lower part of submucous plexus of œsophagus of cat. Stained in methylene blue and fixed in ammonium picrate. Drawn with the aid of the camera lucida under $\frac{1}{6}$ in. objective and 2 in. eye piece. Reduced to $\frac{1}{3}$. *c.*—type I cell, surrounded by end-basket of preganglionic fiber; *p.*—preganglionic fiber; *m.m.*—sensory sympathetic cells; *s.*—sensory cerebro-spinal fiber passing through ganglion; *a.*—non-medullated sympathetic fiber passing through ganglion.

Fig. 5. Tangential section of part of the mucosa of a young cat. Stained in methylene blue and fixed in ammonium molybdate after prefixation for 15 minutes in ammonium picrate. Section about 80μ in thickness. Drawn with the camera lucida, under $\frac{1}{6}$ in. objective and 2 in. eye-piece. Reduced to $\frac{1}{3}$. Shows the end-branching of a large, medullated sensory nerve in the mucosa with the telodendria in the epithelium.

Fig. 6. Surface preparation of one of the end-balls in the upper part of the œsophagus of a cat. Stained in methylene blue and fixed in ammonium picrate. Drawn with the aid of the camera lucida under $\frac{1}{6}$ in. objective and 2 in. ocular. Reduced to $\frac{1}{3}$. Shows medullated nerves, with short medullated and non-medullated branches and telodendria closely crowded together.

Fig. 7. Section through epithelium and part of mucosa of young cat. Stained in methylene blue, fixed for 15 minutes in ammonium picrate and afterwards for 12 hours in ammonium molybdate. Drawn with camera lucida, under 1-12 in. oil immersion objective and 2 in. ocular. Reduced to $\frac{1}{2}$. Shows medullated sensory fibers, subepithelial plexus, and terminal arborization in the epithelium.

Fig. 8. Section through end-ball similar to that in *Fig. 6*. Preparation prepared and sketched as in *Fig. 7*. Shows the rich terminal arborization in epithelium.

THE VIBRISSÆ OF CERTAIN MAMMALS.¹

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Studies from the Hadley Laboratory of the University of New Mexico.

Communicated by C. L. HERRICK.

With Plates XXVII to XXIX.

The lower mammals, in contrast to man, are endowed with a peculiar class of sensory organs developed upon certain modified hairs, the vibrissæ. While these share with the ordinary hairs a tactile function, they differ from the hairs of the general surface not merely by having this common function intensified; but there is a fundamental difference in the way in which the accommodation to that function is accomplished.

President C. L. Herrick has suggested in various papers an intimate relation between vascular changes and the emotional element or tone in sensation and that vascular change may explain periods of latency in the development of pain concomitants of sensation. It was at his suggestion and with a view to the determining whether there was any connection between the vascular mechanism and sensory apparatus of the vibrissa that these studies were undertaken.

Present opportunities prevent any complete canvass of the literature, so that the facts are presented as briefly as possible as a commentary on the plates, which will illustrate the relations in the two types studied.

The tissues were from the muzzle and feet of young dogs and rabbits and were subjected to a variety of treatment in hardening and staining. For our purpose we soon limited the experiment to the rapid Golgi process, iron hæmatoxylin and combined hæmatoxylin and picro-carmin. Of these the Golgi,

¹ In partial satisfaction of thesis requirements for the degree of Master of Arts in the University of New Mexico.

although it proved very fickle, is perhaps most suggestive, especially in revealing the non-medullated fibers and endings, but it would have been insufficient unless supplemented by the other methods. Non medullated nerve fibers were brought out by the Golgi only. The structure of the stroma was shown best by the iron hæmatoxylin, while the hæmatoxylin and picro-carmin gave the arrangement and relation of parts more satisfactorily.

Vibrissæ being modified hairs, the interest centers around the parts most differentiated. At a glance the follicle is seen to be very large and deep and the gland very small.

On closer inspection the absence of erector muscles is noticed, while a somewhat complicated haemostatic apparatus takes their place. The erectile apparatus lies within the corium sheath and, in fact, all the structures peculiar to the vibrissa lie between this sheath and the outer sheath of the hair proper.

A short distance below the gland the hair sheath is enlarged or thickened and above this swelling and between it and the gland is an annular band of nerve fibers encircling the sheath; these are visible in the Golgi preparations and are seen to connect with ascending fibers running parallel to the shaft of the hair.

Encircling the hair and its sheath slightly below the swelling is a body of sponge-like appearance whose structure is, at first, somewhat difficult to make out. This may be called the pulvinus. It is a typical erectile tissue composed of loops of capillaries so arranged as easily to expand when gorged with blood and each capillary is provided with fenestrules through which the blood is permitted to escape into the general lacunal space in which these capillaries lie.

Around the pulvinus is a large space filled to a greater or less extent with a coagulum of lymph and corpuscles. The whole apparatus is therefore an admirable provision for producing a sudden turgor and erection of the capsule and a rigidity of the hair and it can hardly be doubted that the apparatus is under close nervous control.

Nerve fibers penetrate the corium sheath near the base of

the hair and enter in few distinct bundles. They run up along the outer sheath proper of the hair beneath the pulvinus and end in the annular band above mentioned, or rather bifurcate to form that ring. A few nerve fibers are given off to the pulvinus where scattered ganglion cells are demonstrated in Golgi preparations.

The perifollicular space is abundantly supplied with blood vessels and is supported by trabeculæ of connective tissue.

The pulvinus is apparently the chief organ of accommodation. It shrinks during the process of preparation for examination but, no doubt, is much larger when fully distended. The variation in size when prepared in various ways indicates its susceptibility.

The annular nerve band is so situated that when the pulvinus is not turgid tactile impulses are little felt but when it is turgid the slightest impact produces a marked effect on the nerves surrounding the hair.

The most striking feature about the whole structure is the arrangement for blood supply. The animal must be able to control this and thus render his vibrissæ sensitive when he wishes and practicably insensible when he has no use for them. Probably also there is an efficient reflex control.

The number and size of the blood vessels and trabeculæ indicate that the whole space can be engorged with blood almost instantly, affording very efficient erectile tissue in place of the muscles attached to the ordinary hair.

DESCRIPTION OF PLATES.¹

PLATE XXVII.

Fig. 1. Longitudinal section of vibrissa of rabbit. The plane of section lies at one side of the hair and its sheath but shows the corium sheath, stroma, pulvinus, peripulvinar space, gland and nerve bundles.

Fig. 2. Similar section cutting the hair and sheath at base but passing lateral to it at higher levels.

Fig. 3. Similar section showing the relations of pulvinus and peri-pulvinar space. (All the above are hæmatoxylin preparations.)

¹ The figures were all drawn by C. L. Herrick.

Fig. 4. Similar section of dog vibrissa by Golgi method. *g.*—gland; *a.p.*—annular nerve fibers; *x.*—peri-pulvinar space; *P.*—pulvinus; *n.b.*—nerve bundle; *c.h.*—inner sheath; *r.s.*—outer sheath; *H.*—hilum; *o.s.*—corium sheath.

Fig. 5. Golgi preparation as above showing the relation of nerve bundle to annular band (combined from two consecutive slides).

Fig. 6. Cross section of vibrissæ of rabbit near base.

Fig. 7. Portion of same magnified.

PLATE XXVIII.

Fig. 1. Cortex pulvini, rabbit, hæmatoxylin. A close mass of blood corpuscles.

Fig. 2. Surface view of a follicle of a sebaceous gland.

Fig. 3. Nerve fibers near pulvinus with trabecular (erectile) tissue outside.

Fig. 4. Longitudinal section of vibrissa of rabbit at pulvinus. *i.*—hair; *h.*—inner sheath; *g.*—outer sheath; *f.*—nerves above pulvinus; *e.*—trabecule of erectile tissue below pulvinus; *d.*—nerves between pulvinus and sheath; *c.*—pulvinus in shrunken condition; *b.*—cortex, pulvinus, or peri-pulvinar space composed of a coagulated stroma (lymph) with corpuscles; *a.*—corium sheath of vibrissa.

Fig. 5. Capillary in stroma below pulvinus showing fenestrules and imperfect chambers of stroma.

Fig. 6. A part of the nerve ring above the pulvinus.

Fig. 7. Pulvinus lobes in retracted state, blood vessel at base.

Fig. 8. Pulvinus showing entrance of vessels.

Fig. 9. Part of ordinary hair of dog with muscle and motor nerve endings. (Golgi method.)

Fig. 10. A portion of nerve ring, annular fibers.

Fig. 11. A view similar to Fig. 6.

PLATE XXIX.

Fig. 1. Surface view of sheath of vibrissa with longitudinal and annular nerve fibers. Only a few of the sheath cells are sketched in. The arrow shows the direction of the long axis of the hair. (Rabbit.)

Fig. 2. Section of ordinary hair of the muzzle of a dog with muscles and the motor nerve endings. (Golgi method.)

Fig. 3. Similar section of base or bulb of hair with chromatophores upon corium sheath.

Fig. 4. A section of the vibrissa sheath at the point where annular nerve fibers originate (above the pulvinus. Rabbit—hæmatoxylin).

Figs. 5, 6, 8, 9. Ganglion (?) cells from Golgi preparations of the pulvinus of dog vibrissa.

Fig. 7. Ganglion cell (?) in course of nerve adjacent to pulvinus. (Dog—Golgi.)

THE OPHTHALMIC AND EYE MUSCLE NERVES OF THE CAT FISH (AMEIURUS).¹

By I. S. WORKMAN.

With one figure in the text.

In the fishes, as is well known, there are three ophthalmic nerves—the ophthalmicus superficialis facialis (a lateral line nerve), the ophthalmicus superficialis trigemini (general cutaneous), and the ophthalmicus profundus, the latter in some elasmobranchs being a separate nerve arising cephalad of the trigeminus.

The ophthalmicus profundus is typically absent in the bony fishes, the only exceptions thus far recorded being *Trigla* (apparently the root and ganglion only, Stannius '49, p. 25), *Clarias* and *Trichomycterus* (Pollard, '95), *Ameiurus* (Wright '84), *Silurus* (Juge, '99), and probably *Menidia* (Herrick, '99, sec. 7, XI). Allis, however, has expressed doubt as to whether the nerve described by Pollard in siluroids as the ophthalmicus profundus is not really the ophthalmicus superficialis trigemini, and a study of Wright's account of *Ameiurus* led Herrick to the same conclusion.

To clear up this and some other discrepancies in the descriptions of the nerves of the orbit of the siluroid fishes, serial sections were cut through the head of the small stone cat fish, *Ameiurus melas* Raf., and stained by the Weigert process. The results of the examination of these sections were controlled by dissections of the blue fish, *Pomatomus saltatrix* L. The latter is a typical teleost, while it is generally admitted that the cat fishes are decidedly aberrant.

Inasmuch as the distribution areas of the superficial and deep ophthalmic branches of the trigeminus are often very similar (note their peripheral anastomosis in some elasmobranchs),

¹ Studies from the Neurological Laboratory of Denison University, under the direction of C. Judson Herrick. No. XIII.

the most satisfactory criteria of these homologies will be the relations of the ophthalmic nerves to the eye muscles and their nerves and to the other orbital structures, as Allis has employed them in his *Amia* paper. The composition of the nerves proximally cannot be used in any of the higher vertebrates where the profundus has fused with the trigeminus, for both the deep and the superficial branches of the trigeminus in these forms are primarily general cutaneous nerves, and both apparently may carry out also communis fibers from the facial ganglion.

Accordingly, the nerves of the orbit of *Ameiurus* have been plotted on cross-section paper and these relations carefully noted, as well as the exact nature of the termini of such of these nerves as reach the skin. This is one step in a detailed examination of the cranial nerves of American and African siluroids now in progress in this laboratory, and the present account will be confined to the peripheral courses of the orbital nerves after their separation from the ganglionic complex. This complex and its roots have, however, been as fully worked out as our present material will permit and the composition of the rami now under discussion can be stated, if not with absolute certainty, at least with a very high degree of probability.

As indicated above, there are two ophthalmic nerves in *Ameiurus*. The first, or more superficial one, is undoubtedly the *r. ophthalmicus superficialis facialis*. Its fibers separate from the trigemino-facial ganglionic complex earlier than do those of the other ophthalmic nerve and can be traced back into the dorsal lateralis root of the facialis. It receives no other fibers than these and distributes peripherally to the organs of the supra-orbital lateral line and to the pit organs of the top of the head and snout. Its course for its entire length is essentially like that of the corresponding nerve in the other bony fishes.

The other ophthalmic nerve, which, as we shall see, is the *ramus ophthalmicus superficialis trigemini*, arises from the ganglionic complex some distance cephalad of the nerve last described. It receives general cutaneous and communis fibers in approximately equal numbers. The former come from the sensory trigeminus root, a root which, together with the motor

trigeminus, makes up the "supero-lateral strand" of Wright; the latter come from the communis root of the facialis, the "infero-medial strand" of Wright. This nerve, it should be stated, however, separates intra-cranially directly from the ganglionic complex before the two strands described by Wright have been well differentiated and some distance caudad of the point where these strands are re-arranged to form the maxillary and mandibular rami.

The ophthalmicus superficialis V runs forward some distance within the cranium, then passes out laterally through a foramen and continues cephalad running close to the cranial wall over the n. opticus and under the m. dilator operculi. Its first branch, given off soon after its emergence from the foramen, runs out laterally under this muscle and the m. levator arcus palatini, follows the latter nearly to its cephalic end, then breaks up to supply the skin and terminal buds dorsally of the eye, some fibers also running out onto the cornea.

Cross sections of the nerve in this region show two ill-defined groups of fibers. Dorsally the fibers are chiefly of small or medium size, with very many rather coarse ones among them. The ventral half of the cross section is made up almost exclusively of exceedingly fine fibers with a few of medium size scattered among them. The dorsal is probably the general cutaneous portion and the ventral the communis.

A second and smaller branch follows soon after the first and pursues a similar course, some of its fibers, however, turning dorsally to run between the most cephalic tip of the m. dilator operculi and its insertion on the frontal bone. This second branch supplies skin and terminal buds dorsally and in front of the eye.

The main nerve, having meanwhile become separated from the cranium by a slip of the muscle last mentioned near its origin from the cranium, now sends off its third branch, which is much larger than those previously mentioned and which follows a course essentially similar, distributing to the skin of the top of the head farther cephalad than the last. In front of the origin of the levator arcus palatini from the cranium it rises up

and passes through two foramina in the mesethmoid bone to the sub-cutaneous tissue of the top of the head, supplying skin and terminal buds. Its distribution area is altogether in front of the eye and laterally of the nasal sac.

After giving off its third branch, the main nerve rises up nearly parallel with it to the dorso-lateral angle of the supra-orbital cartilage and immediately passes through a foramen in this cartilage and the overlying bone to run under the skin on the dorsal wall of the cranium ventrally and laterally of the r. ophthalmicus superficialis VII. At this level (dorsally of the olfactory bulbs) the nerve gives off several small twigs for the skin and terminal buds of the top of the head in the vicinity of the posterior nasal aperture and then divides into four branches, three of sub-equal size and one much smaller. One of the larger ones, which may be regarded as the main nerve, follows closely the r. ophthalmicus superficialis VII. The other three turn laterally, following the inner wall of the nasal sac, and then all enter the nasal barblet.

The main nerve accompanies the facial ramus of the same name along the inner border of the nasal sac, giving off numerous small branches to the skin and its terminal buds, which are very numerous throughout this whole region. Breaking up into numerous branchlets, it supplies the skin and terminal buds dorsally and mesially of the nasal sac and forward to the tip of the snout—the same region which receives the branches of the r. ophthalmicus superficialis VII for pit organs. The termini of these two ophthalmic nerves interlace freely, but anastomosis occurs but rarely and even then is merely accidental and temporary juxtaposition of the two kinds of fibers of no special morphological significance.

To recapitulate, the ophthalmicus superficialis trigemini arises from the ganglionic complex slightly cephalad and ventrad of the ophthalmicus superficialis facialis, emerges through the cranium by a separate foramen, and pursues an entirely separate course peripherally, lying ventrally of the latter nerve and widely separated from it by the fleshy origin of the m. dilator operculi. In front of the orbit it passes through

a foramen in the frontal bone to run forward close to but distinct from the facial ophthalmic nerve. It distributes to the skin and its contained terminal buds in front of the eye, about the nasal apertures and in front of the latter and to the nasal barblet—about the same distribution, in short, as the fibers of the r. ophthalmicus superficialis facialis destined for pit organs contained in large numbers in this same area of skin. In no case were the fibers of the facial nerve observed to enter terminal buds nor those of the trigeminal nerve to enter pit organs. The trigeminal ophthalmic nerve undoubtedly innervates the skin in general of this area by means of its general cutaneous fibers and the terminal buds by its communis fibers, the large size of the communis component observed to enter the nerve proximally being correlated with the enormous number of buds innervated.

The r. ophthalmicus superficialis V does not run under any of the eye muscles, their nerves or any of the other orbital structures which typically overlie to r. ophthalmicus profundus. It cannot therefore be regarded as the profundus nerve. On the other hand, there are no fibers which can be regarded as the r. ophthalmicus superficialis V save these and their course is the same as that of the latter nerve in other teleosts, save for their separation from the facial ophthalmic nerve by the origin of the m. dilator operculi, which extends very far forward in Ameiurus.

The *infra-orbital trunk* comprises the r. buccalis (for the infra-orbital lateral line canal) and the maxillary and mandibular nerves. These three nerves soon separate from each other, but run parallel for a short distance.

The maxillary and mandibular nerves have the typical teleostean composition, receiving the motor trigeminal root (r. mandibularis) and the major parts of the general cutaneous trigeminal and the communis facial roots. These two latter roots run directly cephalad from the ganglionic complex into the infra-orbital trunk, having previously given off several branches dorsally (the r. lateralis accessorius of communis fibers, dorsal general cutaneous twigs, and the r. ophthalmicus superficialis V,

composed of both communis and general cutaneous fibers). The communis root constitutes the "infero-medial strand" of Wright, the general cutaneous root (together with the motor V) the "supero-lateral strand." These two strands remain distinct until after the trunk has emerged from the cranial wall, then their fibers are re-arranged so that both maxillary and mandibular nerves receive general cutaneous and communis elements in approximately equal proportions.

At the level of the optic nerve from its foramen, these nerves are arranged ventrally of that nerve and of the great levator arcus palatini muscle, mesially of the m. adductor mandibulæ and dorsally of the m. adductor arcus palatini, the r. mandibularis being external, the r. maxillaris internal and the r. buccalis dorsally and between the other two.

Considerable importance to phylogeny having recently been attributed to the eye muscle nerves, we have carefully worked them out.

VI. The abducens arises by several rootlets and runs forward just internal to the VIII nerve and ganglion. Continuing in the same direction, it comes to lie at the ventral angle of the geniculate ganglion. It now applies itself to the fiber complex arising from this ganglion, the "infero-medial strand" of Wright, becoming embedded in its ventral and inner edge, though always clearly distinguishable by reason of the larger size and heavier myelination of its fibers. As the infra-orbital trunk passes through its foramen in the cranial wall, the VI nerve runs up along its inner face to join the III nerve, parallel with which it runs out for some distance, as mentioned by Wright. It then passes directly outward close above the infra-orbital trunk and under all of the other orbital structures to enter the rectus externus at its posterior margin in the typical way.

IV. The trochlearis immediately upon its exit from the brain applies itself to the inner face of the V + VII ganglionic complex and follows the same forward, accompanying the r. ophthalmicus superficialis V along its ventral edge until it has emerged through its foramen into the orbit. It now lies in the

narrow space between the r. ophthalmicus superficialis V dorsally and the optic nerve ventrally, then turns gradually outward under the m. adductor arcus palatini, continuing to lie slightly ventrally of the ophthalmicus superficialis V and dorsally of the other orbital structures until it enters the superior oblique muscle.

III. The oculomotorius likewise immediately upon its exit from the brain is crowded close up to the ganglionic complex, following its innermost angle close below the fourth nerve until the r. ophthalmicus V separates from the rest of the complex. The oculomotorius now turns outward under the ramus last mentioned closely followed by the abducens, emerging from the cranial foramen dorsally of the latter and internal to the infra-orbital trunk. It now runs out cephalad and laterally over the infra-orbital trunk and dorsally and laterally of the VI nerve, the two being bound up in the same sheath, and divides into two unequal portions, the smaller one being dorsal. The smaller branch runs out under the superior rectus muscle, which it innervates, crossing over the other rectus muscles.

A short distance cephalad the third nerve again divides, the two branches, along with the sixth nerve, here being crowded in between the infra-orbital trunk, lying ventrally, and the m. rectus superior. Further cephalad the m. rectus externus slips in below them and the m. rectus inferior lies above the more mesal branch, the lateral branch supplying this muscle. The mesial branch runs cephalad under m. rectus internus, where it divides, sending one branch directly dorsad to innervate this muscle, the remainder continuing cephalad in the original position to supply the obliquus inferior.

Wright states ('84, p. 365) that in *Ameiurus catus* the ventral branch of the oculomotorius runs over the rectus inferior and rectus internus, while Allis ('97, p. 520) says that the ventral branch runs ventrally of these muscles in *Ameiurus*. Allis does not mention the species of *Ameiurus* which he dissected, but presumably it was *A. catus*. Our examination of *A. melas* confirms Allis' account, rather than Wright's. The relations of the organs described in *Ameiurus melas* are illustrated by the accompanying diagram, which should be compared with the similar diagrams given by Allis ('97, Fig. 12) and with the diagrams of *Menidia* and *Amblystoma* by Herrick ('99, Figs. 13 and 14). It will be noticed that the arrangement in *Ameiurus* corresponds to the ganoidean arrangement as given by Allis, rather than to the teleostean arrangement as

given by Herrick for Menidia. Allis assumed that Ameiurus gives the typical arrangement for the teleosts, while Herrick assumed that Menidia does so. Our study of the blue fish, Pomatomus, tends to support the latter conclusion, as the ar-

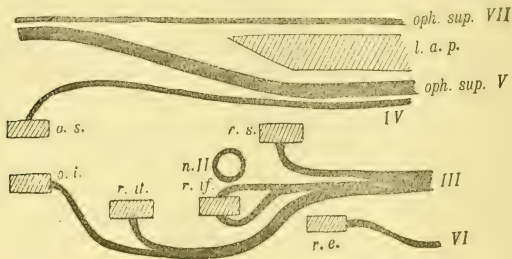


Diagram of the orbital nerves of *Ameiurus melas*. Reference letters :

III.—n. oculomotorius.

IV.—n. trochlearis.

l. a. p.—m. dilator operculi.

n. II.—optic nerve.

o. i.—m. obliquus inferior.

oph. sup. V.—ramus ophthalmicus superficialis trigemini.

o. s.—m. obliquus superior.

r. e.—m. rectus externus.

r. if.—m. rectus inferior.

r. it.—m. rectus internus.

r. s.—m. rectus superior.

VI.—n. abducens.

rangement of the orbital nerves in *Pomatomus* is identical with that of *Menidia*, save for the absence in the blue fish of the supposed rudiment of the profundus nerve described for *Menidia*. Herrick (1900, p. 295) has also found the same conditions to prevail in *Gadus*.

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ON THE HOMOLOGIES OF THE CHORDA TYMPANI IN SELACHIANS.¹

By H. A. GREEN.

With three figures in the text.

Probably few nerves in the human body have given anatomists and morphologists more trouble than the chorda tympani. In the first place the true course of the nerve has long baffled anatomical researchers, and on the other hand any one of the possible paths which these fibers may take presents peculiar difficulties of morphological interpretation.

It will be recalled that the posterior part of the tongue is innervated by the gustatory part of the glossopharyngeus nerve, while the anterior part is supplied by the lingual nerve, which is composed chiefly by the lingual branch of the trigeminus, to which is added the chorda tympani, and an unknown number of sympathetic fibers. Without attempting to summarize at this time the exceedingly diverse views which have been held regarding the courses of the fibers in these nerves, and confining our attention to the gustatory fibers in the lingual nerve, the weight of authority at the present time is clearly in favor of regarding these as derived from the chorda and of denying the gustatory function to any of the trigeminus roots. The lingual branch of the trigeminus is, then, devoted to general sensation of the tongue, while the sense of taste is mediated by glossopharyngeal and facialis fibers. While there is some clinical evidence on the other side, the weight of evidence (particularly anatomical and embryological data) favors this view.

The geniculate ganglion of the facialis being a typical

¹ Studies from the Neurological Laboratory of Denison University, under the direction C. Judson Herrick, No. XIV.

cerebro-spinal ganglion, the central processes of its cells enter the portio intermedia of Wrisberg and the fasciculus solitarius to terminate with the gustatory fibers of the glossopharyngeus in the associated grey matter. The peripheral processes of these geniculate ganglion cells in part enter the great superficial petrosal nerve and in much greater number the facialis trunk. Most of the latter fibers leave the trunk within the Fallopiian canal and pass back by a separate canal in the temporal bone to cross through the tympanic cavity and join the lingual branch of the trigeminus for taste buds on the tip of the tongue. This is the chorda tympani. A much smaller number of sensory fibers has recently been shown to remain in the facial trunk after the separation of the chorda.

This, I think, may fairly be said to represent the consensus of recent opinion. Its receives strong confirmation from the study of the comparative anatomy of the facial nerve; and not only so, but its morphological interpretation, as well.

It is now pretty generally recognized that the facial nerve of fishes is a very typical branchial nerve, in selachians branching around the spiracular cleft as the IX and X nerves fork around their respective gill clefts and sending forward a palatine branch corresponding to the r. pharyngeus of the other branchial nerves.

The composition of the branchial nerves in the fishes can be stated with precision. The post-trematic branch runs down behind the cleft to supply the half gill on its posterior wall and the muscles of that arch. It is, therefore, of mixed motor and sensory function. The pre-trematic branch supplies the half gill in front of the cleft and the pharyngeal, or palatine, branch the mucosa of the roof of the pharynx adjacent, both of the two latter being wholly sensory. All of the sensory fibers belong to the communis system, fibers associated with the fasciculus communis (f. solitarius) and its terminal nuclei and supplying visceral surfaces and taste buds. The motor fibers belong to the visceromotor system innervating the branchial musculature or its derivatives. The facialis conforms exactly to this scheme, save that in all fishes the post-spiracular half gill

has disappeared and the pre-spiracular or mandibular half gill has in most cases been reduced to a vestigial condition, the pseudobranch.

Even in man these relations are not wholly obscured; for here we can recognize the main facial trunk as homologous with the post-spiracular ramus, the great superficial petrosal as the palatine branch and the chorda tympani as a probable pre-spiracular ramus. These homologies are fairly well established, in the various groups of lower vertebrates; except in the case of the chorda, but on the latter point there has been the greatest diversity of opinion.

Now, first, what are the criteria of the chorda tympani? As to its composition, it is in part, at least, a gustatory nerve and therefore belongs to the communis system of nerves as defined by Strong. As to its course, it forms a part of the sensory facialis root, its fibers are related to cells to the facialis (geniculate) ganglion and they pass out by a circuitous course above and in front (cephalad) of the middle ear and Eustachean tube, then downward along the inner side of the mandible to enter the tongue from the side. Remembering that the Eustachean tube is the phylogenetic derivative of the spiracular canal and that the tongue is built upon the hyoid arch, it is obvious that the chorda is one of the pre-spiracular branches. It has been assumed by some authors who hold this view (e.g., Cole) that it represents the pre-trematic ramus of the fishes in the strict sense, viz., the branch for the gill on the anterior face of the spiracular cleft, or mandibular hemibranch. Stannius, however, has given an account which would seem to put the matter in a slightly different light. In his great monograph on the peripheral nervous system of fishes, published in 1849, he describes for *Raja* and *Spinax* three pre-spiracular twigs, as follows:

“Der N. palatinus ist bei *Raja*, wie bei *Spinax*, complicirter, als bei den Knochenfischen. Er wird durch drei Zweige repräsentirt: einen zarten hinteren und zwei stärkere vordere, welche bei *Raja clavata* und *R. batis* ein zehr zierliches Geflecht bilden.

“ 1) Der hintere Zweig ist wesentlich für die Pseudobranchie des Spritzloches bestimmt. Er entsteht bei *Spinax* mit zwei Schenkeln, welche später sich vereinigen, geht schlingenförmige Verbindungen ein mit Fäden des zweiten Astes, begibt sich, neben der von der Pseudobranchie kommenden *Vena arteriosa* gelegen, zum Spritzloche und verläuft längs der Pseudobranchie bogenförmig aufwärts.

“ 2) Der erste vordere Zweig ist wesentlich für die Schleimhaut der Mundhöhle bestimmt. Nachdem er einen Faden für die membranöse Vorderwand des Spritzloches nach hinten abgegeben, der mit dem Nerven der Pseudobranchie schlingenartig sich verbindet und bald derauf auch mit dem dritten Zweige oder dem eigentlichen *Ramus palatinus* schlingenartige Verbindungen eingegangen ist, strebt er, einen Bogen bildend, an der zwischen Zungenbein und Unterkiefer liegenden Schleimhaut der Mundhöhle abwärts und einwärts, wo denn einzelne Zweige die ventrale Mittellinie erreichen. Die fortsetzung des Stammes gelangt zur Verbindungsstelle von Oberkiefer und Unterkiefer, verläuft dann an der den Unterkiefer inwendig auskleidenden Schleimhaut und erstreckt sich mit seinen Zweigen, welche mit denen des *Ramus mandibularis* vom *N. facialis* Schlingen bilden, bis zur Mittellinie des Unterkiefers.

“ 3) Der zweite vordere Zweig ist der eigentliche *Ramus palatinus*.”

From this it appears that these selachians possess, in addition to the *R. palatinus* and the true pre-trematic ramus for the mandibular hemibranch, a third pre-spiracular nerve, which runs out between the other two along the anterior lining of the spiracular cleft, then forward and inward under the mucous lining of the mouth between the hyoid and the mandibular arches reaching to the ventral median line. This nerve perfectly fulfils all of the requirements of a *chorda tympani*. Its origin with the palatine and other pre-spiracular nerves indicates that it is of *communis* nature, a supposition which is confirmed by its peripheral course, and its peripheral distribution is just as in the human body, save that the absence of the fleshy tongue

in the fishes precludes its anastomosis with a lingual branch of trigeminus, that nerve not being present in the lower vertebrates.

These homologies were suggested by Herrick in his *Menidia* paper in 1899, where he has discussed the literature in some detail.¹ The description of Stannius seemed so fruitful in suggestions that we have examined some other selachians with a view to confirming and extending his observations.

In *Squalus acanthias* we find the conditions corresponding to the description of Stannius, quoted above, almost exactly. The foramen through which the hyomandibular root passes out of the cranium is quite long and the swelling which corresponds to the geniculate ganglion lies far out on the root. Stannius found upon microscopical examination that this swelling in selachians contains ganglion cells. From it a large bundle of fibers is given off into the hyomandibular trunk, the same fibers undoubtedly which peripherally compose the r. mandibularis internus. We also confirm Stannius' description of this nerve. It separates from the trunk near the outer edge of the hyomandibular cartilage and curves inward and forward along the outer face of the hyoid arch under the mucosa of the mouth to the end of that arch then runs forward to the lining of the mouth over the tip of the mandible. It is apparently purely sensory.

¹ Some of the more important articles which have appeared since that paper are as follows.

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The pre-spiracular branches of the facialis are given off together from the geniculate ganglion. All of these fibers appear to arise from this ganglion, i.e., to be of communis nature, though this point cannot be certainly determined in the absence of microscopical examination. The palatine is the largest of

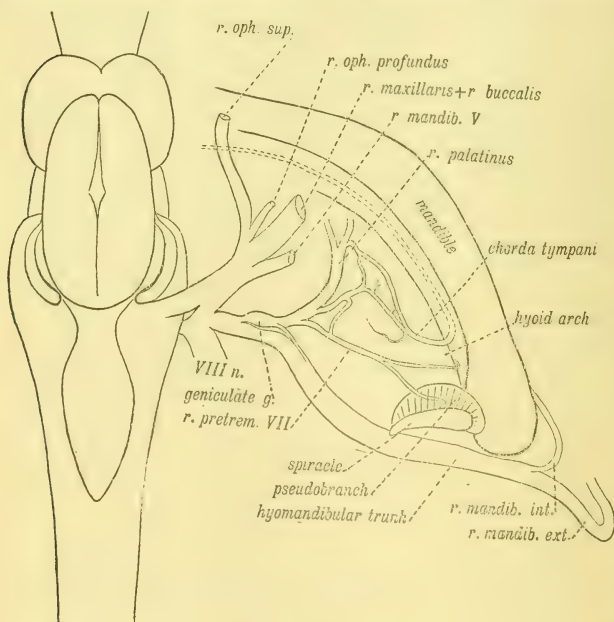


Fig. 1. Dissection of the facial nerve of the spiny dog shark, *Squalus acanthias*, L., as seen from above, the eye and palato-quadrate bar having been removed. $\times 2$. The figure shows the mode of origin of the chorda tympani and its course to the inner edge of the lower jaw. Its further course on the ventral surface is indicated by the dotted line between the mandible and the hyoid arch, only a part of the outer border of the latter being indicated.

them and the r. pre-trematicus in the strict sense is the first branch to be given off, the chorda tympani separating somewhat farther distally. The pre-trematic ramus in this specimen arises by one root and the chorda by two, these all anas-

tomosing with each other. The details of this anastomosis are not exactly the same on the two sides of the specimen so far as the smallest twigs are concerned, though the larger ones on both sides are as figured. The chorda after the union of its two chief roots runs down around the edge of the hyoid arch to the ventral surface in the space between the latter arch and the mandible, then running forward and inward along the inner face of the mandible, keeping all of its course close under the mucous lining of the mouth, until it reaches the ventral median surface under the tip of the mandible. Its principal distribution seems to be to the strong crescentic fold of the mucosa which projects up into the floor of the mouth just behind the teeth of the lower jaw. Near the median line it anastomoses with the terminal twigs of the r. mandibularis internus of the facialis, as Stannius mentions.

In the sand shark, *Carcharis littoralis*, we find the conditions indicated on Fig. 2. The post-spiracular and pre-spiracular nerves go out from the brain together for a short distance, then the post-trematic, or hyomandibular trunk, turns caudad and the palatine nerve cephalad. From the base of the palatine four twigs are given off directed laterally. The first of these is the true pre-trematic branch, which runs backward along the caudal face of the upper jaw embedded in the mucous membrane which forms the anterior (cephalic) wall of the spiracular cleft. Here it divides, one twig passing directly to the pseudo-branch, under which it breaks up, the other twig running a little farther ventrally to supply the mucosa of the outer part of the anterior wall of the spiracle adjacent to the pseudo-branch.

The second branch runs out laterally to the edge of the roof of the mouth, where it turns down to supply the adjacent mucosa. It is to be regarded as a detached filament of the r. palatinus.

The third and fourth branches run out laterally to the inner surface of the palato-quadrato and then unite, afterwards pursuing a course approximately parallel with that of the pre-trematic ramus, but farther ventrally. Running back along the

inner face of the palato-quadrato and in front of the spiracular cleft, just in front of the point of articulation of the mandible it turns inward in the mucosa of the pharynx to the point where the hyoid and mandibular arches separate. Here the nerve breaks up. Most of the fibers appear to run forward

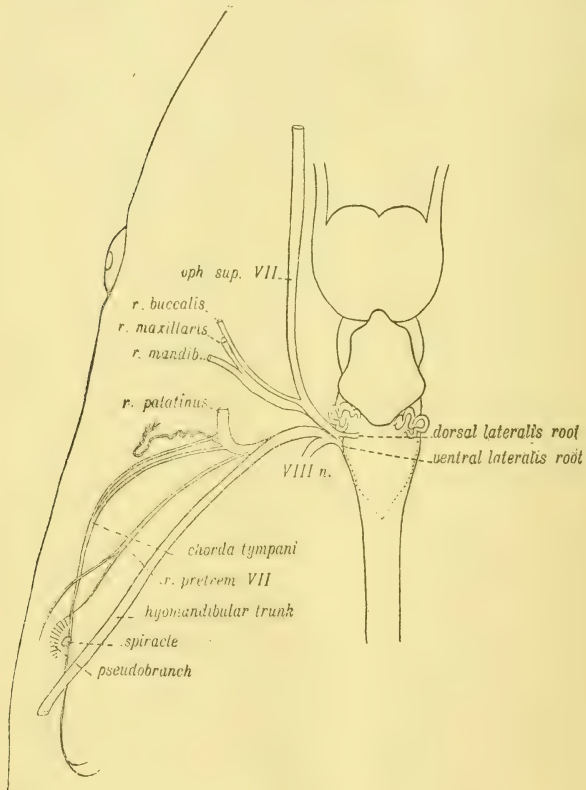


Fig. 2. Dissection of the facial nerve of the sand shark, *Carcharias littoralis*, Mitchill, from above. Natural size.

on the inner face of the mandible, though some may also go out on the hyoid.

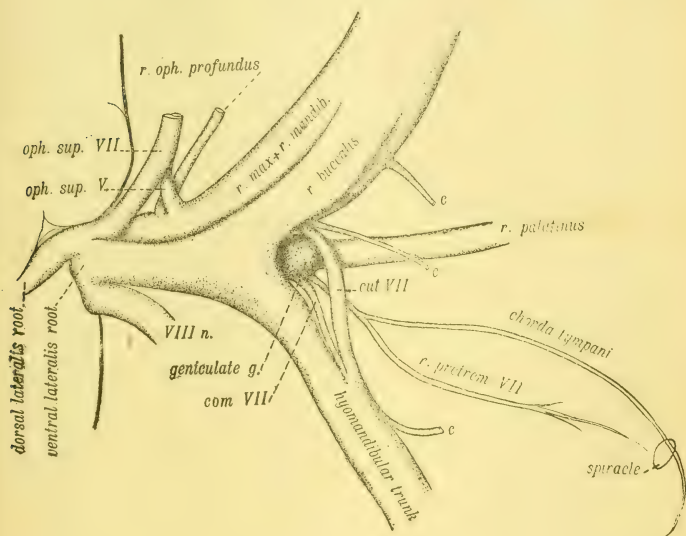


Fig. 3. Dissection of the trigemino-facial roots of the right side of the smooth dog shark, *Galeus canis*, seen from above. $\times 2$. *c, c, c*, general cutaneous twigs for the skin of the caudal border of the orbit. *com. VII*, communis fibers from the geniculate ganglion to the hyomandibular trunk. *cut. VII*, general cutaneous fibers from the trigeminus to enter the hyomandibular trunk, displaced outward during the dissection so as to expose the geniculate ganglion.

These relations correspond to those of *Squalus acanthias* save that we have not succeeded in following the nerve regarded as the chorda so far downward as to reach the ventral median line. Its proximal connections could not be made out, as the several ganglia of the V + VII complex cannot be clearly separated by gross methods in *Carcharias*. Their origin from the base of the palatine, which is known to be a communis nerve, would, however, strongly indicate that they too are communis nerves.

In the smooth dog fish, *Mustelus canis*, the proximal relations are much clearer (Fig. 3). Here the acustico-lateral, general cutaneous and communis ganglia of the trigemino-facial complex can be quite sharply analyzed by simple dissection. The acustico-lateral system lies dorsally to the others so as to obscure the relations somewhat, but the figure shows the roots and ganglia in their normal relations save that the general cutaneous branch, *cut. VII*, for the hyomandibular trunk has been displaced laterally to expose the geniculate, or communis ganglion of the facialis. The pre-trematic ramus and chorda tympani are seen to arise together from this ganglion independently of the palatine ramus. *Mustelus*, it will be recalled, lacks a spiracular pseudobranch, but the pre-trematic ramus, after giving off several twigs for the mucosa of the anterior wall of the spiracle, terminates in the exact region where it would be if it were present. The chorda curves around the anterior wall of the spiracle to the point of divarication of hyoid and mandibular arches just as in *Carcharis*.

It will also be noted in this dissection that the geniculate ganglion clearly sends a branch backward into the hyomandibular trunk, showing that here, as in *Squalus acanthias*, this nerve contains visceral sensory fibers in addition to the lateralis and motor components, while the branch, *cut. VII*, referred to above, seems to carry general cutaneous fibers from the Gasserian ganglion into it also. Whether the geniculate ganglion contributes to the maxillary or mandibular rami of the trigeminus could not be determined.

The spiracular nerves of the common skate, *Raja erinacea*, and of *Torpedo ocellata*, were also examined, but in these cases the nerves corresponding to what we have termed the chorda were less perfectly developed than in the other species and they could not be traced far down toward the ventral surface.

It is obvious that the facialis of fishes departs from the typical arrangement of branchial nerves by reason of the loss or reduction of the hemibranchs primitively innervated by its post- and pre-trematic branches. The post-trematic, or hyo-

mandibular ramus receives the typical motor and communis roots and in addition secondary accessions from the acustico-lateralis and general cutaneous systems. Its gill has disappeared completely, but the arch has been enlarged and accordingly the nerve runs far out onto the hyoidean apparatus, some of its branches also extending still farther to the tip of the mandible. This last applies also to its cenogenetic additions, notably the lateralis component. The anterior hemibranch of the facialis segment is either absent or greatly reduced. In either case its nerve persists in a vestigial condition. The pharyngeal branch is present and of typical composition, but enlarged, so as to extend far cephalad of its segment into the anterior part of the mouth cavity as the r. palatinus. Between the pre-trematic and palatine nerves another has been interpolated in the facial segment, which runs forward between the hyoid and mandibular arches. It may be extended out upon the mandible in the lower vertebrates, but in the higher it is extended out upon the hyoid and in forms which possess a fleshy tongue it joins the lingual branch of the trigeminus to innervate this organ, thus forming the chorda tympani. The motive for the forward extension of all of these facial branches is the same; viz. the forward growth of the facial skeleton in gnathostomes and the necessity for the innervation of the sense organs about the mouth from the post-oral segments. The evolution of a chorda tympani is only one incident in this progressive specialization of the oral region.

Our especial thanks are due to the U. S. Fish Commission and the director of its Woods Hole Laboratory, Dr. Bumpus, for the facilities for this research and for many special courtesies. We are also indebted to Dr. R. R. Bensley of the University of Toronto and to Mr. B. A. Bensley of Columbia University for important dissection material.

EDITORIAL ANNOUNCEMENTS.

The editors are certain that the readers of the JOURNAL OF COMPARATIVE NEUROLOGY will join with them in cordially welcoming to the board of editorial collaborators, DR. LEWELLYS F. BARKER, *Professor of Anatomy in the University of Chicago and Rush Medical College*. The department of neurology of which Dr. Barker will have especial editorial supervision is, The Neurone Systems and Conduction Paths, a department of which the basis of our knowledge has been revolutionized within the past decade and of which our exact knowledge of anatomical fact has in large measure been acquired within the same time. Dr. Barker is peculiarly well qualified to serve us in this field, for he not only stands at the fore among those who have contributed to our knowledge from these newer points of view, but he has shown an ability rare among his colleagues of correlating the new with the old, and thus performing a double service. For many of us are apt to forget that nearly all of the generalizations now currently included in the so-called "neurone theory" were suggested more or less definitely by the researches of what might be called the pre-Golgi neurologists, particularly those working with the various degeneration methods.

In conformity with the present purpose of the editors of giving from time to time synthetical reviews and digests of neurological literature, the first number of Volume XI will contain a complete bibliography of the literature on the organ and sense of smell, by DR. H. HEATH BAWDEN of the Department of Philosophy of the University of Iowa. This bibliography will contain nearly 1000 titles, including anatomical, physiological and psychological subjects.



Fig. 1.

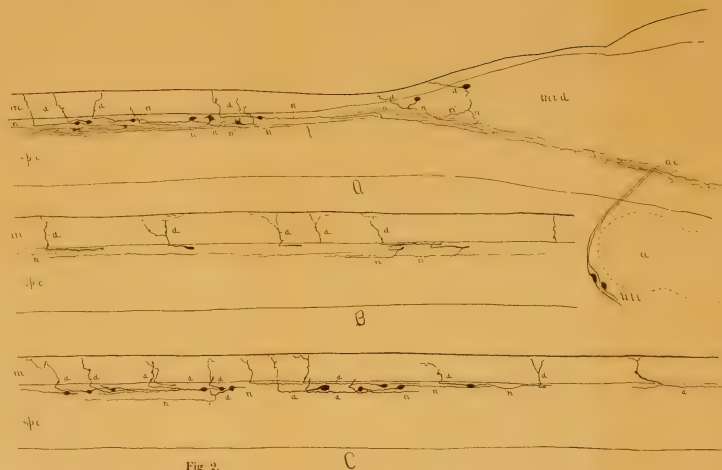


Fig. 2.

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Fig. 3.

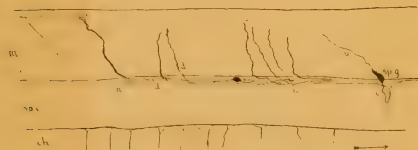


Fig. 4.

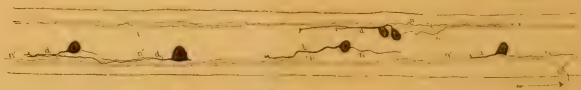


Fig. 5.



Fig. 6.



Fig. 7.



Fig. 8.

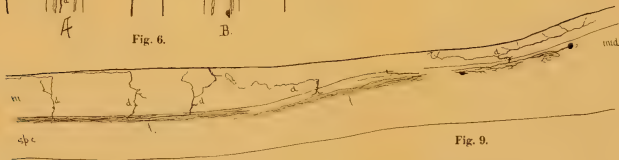
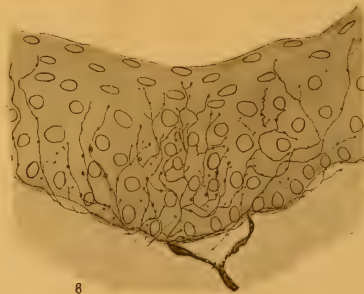
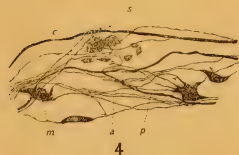
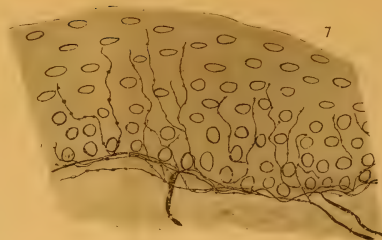
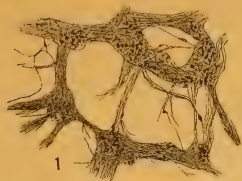
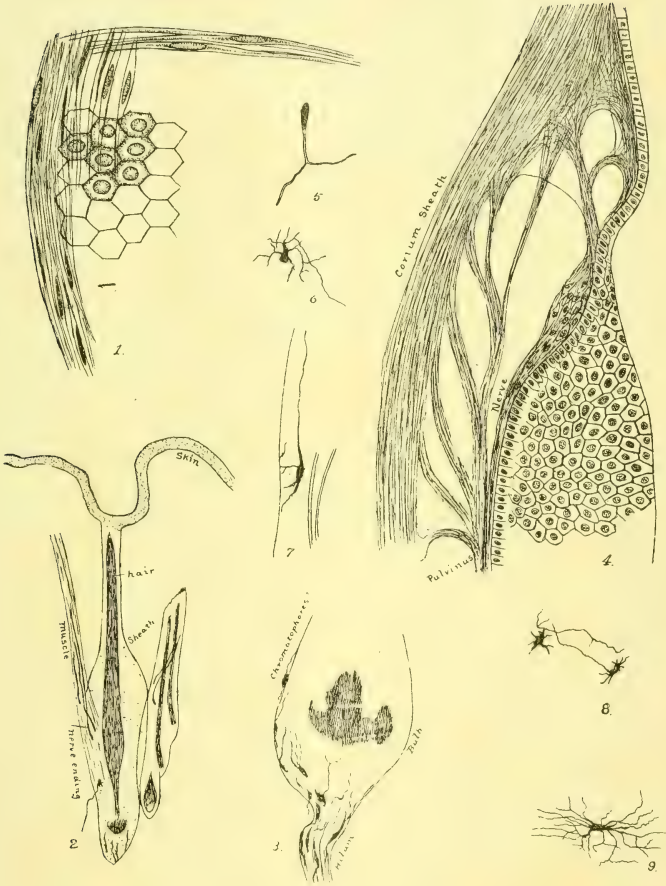


Fig. 9.









LITERARY NOTICES.

REVIEW OF RECENT TEXT-BOOKS OF ANATOMY AND PATHOLOGY OF THE NERVOUS SYSTEM.

SECOND ARTICLE.

Church and Peterson's Text-book.¹

"This book has been written for medical students and general practitioners. It makes no claim to be other than a carefully prepared text-book. The literature of neurology and psychiatry has been sifted by the authors, and such digest revised in the light of their own experience in practice and in teaching."

Church starts from the methods of examination of patients (pp. 17-69), which are presented clearly and concisely. Then follow the descriptions of the various diseases, of the cerebral meninges and cranial nerves (pp. 70-154); of the brain proper (pp. 155-259); of the spinal meninges and the spinal nerves (pp. 260-315); of the cord proper (pp. 316-433); then diseases of the general nervous system with anatomical basis (pp. 434-455) and diseases of the nervous system without known anatomical basis (pp. 456-585) and finally symptomatic disorders (pp. 586-600).

Opinions may well be divided as to what is the best classification of the material for a text-book. The use of the coarse anatomical distributions of lesions as a fundamental principle will appeal to many students, since examinations are apt to lay stress on such questions. For the logical thought of a physician, confronted with broad pathological problems, this method seems, however, less advantageous. The various chapters are well and lucidly presented and the promise given in the preface is well lived up to. The numerous illustrations are well chosen. Many objects and patients are shown in a number of views which give vivid pictures rarely found in equal quality in text-books.

Dr. Peterson gives a picture of psychiatry, based on his clinical lectures and embodying "only the facts which I believe to be most

¹ *Nervous and Mental Diseases*, by Archibald Church and Frederick Peterson. With 305 illustrations. 843 pp. W. B. Saunders, Philadelphia, 1899.

serviceable and useful to those who are often practically concerned with the early diagnosis and prognosis of insanity." After the usual definitions and the enumeration of a few "classifications" (pp. 603-610), the author takes up the general etiology of insanity (pp. 610-647). Twenty-one out of these 37 pages are devoted to a summary of the stigmata of degeneration, practically a reprint of Peterson's article in the *State Hospitals Bulletin*, 1896, illustrated by 34 figures. The space allowed to the other far less problematic and decidedly much more essential etiological factors is very short and in many respects failing to give a fair picture to the student. Alcohol gets 28 lines, syphilis, 22, while the relatively unimportant "imitation" gets over 3 pages with 4 detailed observations.

General Symptomatology is dealt with on pp. 648-676. Peterson follows closely the descriptions given by Ziehen; i. e., the most diagrammatic and lifeless exposé of the topic ever produced. It is difficult to see what satisfaction the student will carry away from this pseudo-psychology. It looks very plausible and systematic at first sight; but it has not a shadow of a connection with the subsequent clinical descriptions and problems.

Chapter IV (pp. 676-680) gives an outline of the course of an examination and a few remarks on the course and prognosis of mental diseases. Chapter V (pp. 680-693) outlines the general treatment of insanity.

The subsequent chapters deal with the individual disease-types. Mania is dealt with in 6 pages, melancholia in 10, circular insanity in 6, epilepsy in 8, dementia in 5, general paralysis in 13, paranoia in 24 and idiocy covers 50 pages. The length of the chapters is proportionate, not to the importance of the topic, but to the reprints of previous articles on special questions by the author. This is decidedly to be regretted.

The reviewer recognizes the difficulty of writing a text-book on mental diseases at this juncture of psychiatry; but even with this admission we cannot say that the present attempt gives even a representative idea and certainly no inspiring outlook of what psychiatry is worth and is striving for.

The clinical descriptions, as far as they go, are concise and well written as may well be expected from the clear and fluent style of the author; yet the book makes one feel that the truly brilliant philanthropist and able neurologist and essayist left his strongest ground and yielded too readily to the publishers who made him undertake the most difficult task medicine presents today. When Dr. Peterson's

grand effort to have psychiatric clinics established in all the larger cities will produce better means for a clinical treatment of the subject, it will probably be easier for him to produce a live picture of the results and problems of psychiatry. Between traditions and impressionist methods, the general pathology of mental diseases has a long and agitated infancy.

ADOLF MEYER.

Brain Weight and Mental Capacity.

From the first dawn of anatomical knowledge theories as to the relation between the brain and intelligence have possessed a peculiar fascination for the student. Even where it has not run into such fantastic extremes as phrenology and the early forms of localization, the idea that there is some relation between the quantity of brain substance and the psychic endowments of man has dominated our literature. It is true that the few data that have been collected seem to show that such a relation is far from constant. Among ethnologists it has come to be an accepted dictum that, other things being equal, the brachycephalic skull is characteristic of a higher intellectual development than the longer, narrower skull. Some eminent men have been blessed with extraordinary brain capacity and weight and a number have had the way paved for this development by a skull-stretching attack of hydrocephalus in youth.

Nevertheless it is evident from the results of histological study that there are other factors of greater moment than the actual or even the relative size of the brain. It is difficult also to make the correct allowance for the ratio of brain and body development. From all analogy we should expect that the proportion between the size of the brain and that of the body would be higher in short than in tall persons. Francis O. Simpson, in the *Journal of Mental Science* of October, 1898, discusses the specific gravity of the insane brain, basing his work on the earlier paper of Sonkey.¹ Sonkey stated that the specific gravity of the normal brain is, for the gray matter, 1034 and, for white matter, 1041. Simpson made a series of determinations from the brains of subjects who had died of general paralysis, senile dementia, and other chronic degenerations and found that, while the specific gravity varies in different parts of the brain, the gray substance averages 1039 in men and 1032 in women, while the white averages 1041 in both sexes. From this it would appear that the difference between

¹ *Brit. and Foreign Medico-Chirurg. Rev.*, 1853.

the sexes is greater than any difference that can be recognized between the healthy and diseased brain.

This question of the relation of brain to mental development receives new interest from the recently published accounts of the brain of Professor v. Helmholtz, whose death occurred from the results of a paralytic stroke due to hemorrhage into the right hemisphere. A full account of the anatomical examination is given by Dr. David Hanseman in the *Zeits. f. Psych. Phys. Sinnesorgane*, XX, 1, from which the following data are taken.

With a hight of 169.5 cm. the cranial measurements were, circumference, 55 cm., length, 18.3, width, 15.5, index, 85.25, figures indicating a hyperbrachycephalic skull. Weight of brain, 1700 gr. including contained blood, but it is estimated that without the extravasated blood the weight would be about 1440 gr. The right hemisphere, with the exception of the frontal, parietal and occipital lobes, was nearly wholly destroyed and the hemorrhage had found its way into the ventricle. The vessels at the brain base were sclerosed, though unequally so. Although the skull showed marked evidence of senile atrophy, the brain was free from such signs. As already said, from the evidence at hand it appears that very little reliance can be placed upon the size and weight of a brain as an index to the perfection of the functioning of the organ, and far greater significance attaches to the configuration of the convolutions. In the brain of Helmholtz the gyri were highly developed. The frontal lobe especially had a very complicated pattern. The lower part of the parietal convolution is strongly developed, especially that part between the gyrus supramarginalis and the third occipital convolution. The precuneus is also unusually pronounced and complex.

The author attempts to show that the parts chiefly developed are such as correspond to the association spheres as defined by Flechsig. It is, of course, hard to begin the examination of the brain of a noted man with entire objectivity and it must be admitted that similar conditions of the brain surface may be found in the case of those who have never emerged from the level of sheltering obscurity. It must also be remembered that a mind like that of Helmholtz might, if directed in other lines of activity, scarcely have attained to a greater recognition than that of many another man regarded as simply clever.

Another point touched upon in the article referred to is the effect of early and transitory hydrocephalus in preparing the way for unusual brain development. Intracranial pressure due to results of such disease, the author thinks, may be an adequate occasion for heightened

brain functioning. At any rate Helmholtz adds another to the rather suggestive list of great thinkers who carried through life the marks of an early attack of hydrocephalus.

In this connection attention may be called to a set of facts in themselves well enough known but which seem to be singularly ignored by pedagogic writers and practical psychologists. It is a fact of everyday knowledge that many forms of functional disorder, those that cannot be regarded as really pathological, such as the exhaustions and perturbations of puberty and the effects of excessive fatigue or worry, produce slight abnormalities in the sense-organs as well as in the central system. These we detect in the day time as *muscæ volitantes* in the eyes, as tension and subjective sounds in the ears, as formiculating distress in the skin, and pruritis, as well as all sorts of hyperæsthesias of all the senses. At night these physiological irritants reveal themselves in the form of pictorial illusions composed by the phantasy upon the basis of these sensory stimuli. The sense element gives to such images a degree of objectivity so that the pictures move with the motion of the eyes and vary with the changes in the stimulus. It is of such material that the foundation of dreams is laid. Now if the comparatively slight physiological changes mentioned are competent stimuli for determining brain activity, how much more those constant or intermittent stimuli resulting from some hidden source of irritation. The irritability growing out of the suppression of certain important functions of the body has been responsible for many a poem and work of art, just as the irritation of the menopause has given us agitators of sundry remarkable reforms or instigated fanatical anti-vivisection campaigns.

C. L. H.

Fere—L'instinct sexuel.¹

This volume is a pleasant contrast to much of the recent literature upon this and related subjects. It is a healthful, clean and thoroughly practical book dealing frankly and yet tactfully with problems of the greatest importance to sociology, morals and practical philanthropy. The author's main thesis is to demonstrate that the sexual instincts, both in their normal and in most of their pathological phases, have not that inflexible coercive power over the individual which some authors would claim for them. He insists that they are amenable to control, and he puts this control where it belongs—with the individual.

¹ L'instinct sexuel, évolution et dissolution, par le Docteur CH. FERÉ, médecin de Bicêtre. 1 vol., 12 mo., pp. 246; 4 fr. (Paris, Félix Alcan éditeur.)

We have not seen in recent medical writings a stronger plea for public and personal morality, and that too aside from the great weight given by the author's high professional standing. The chapters are the following: The first two, devoted to the evolution and dissolution of the sexual instinct, are followed by an interesting account of sexual perversions in animals, and this by anomalies of parental affection in man and anomalies of the sexual instinct in man (three chapters). One chapter is devoted to inversion and one to symptomatic perversions. The remaining chapters are devoted to, somatic and psychic affections accompanying or following sexual relations, predisposition and exciting causes in the etiology of sexual perversions, the offspring of the sexually abnormal, sexual education and hygiene (a very practical discussion), and responsibility and anomalies of the sexual instinct. C. J. H.

Jahresbericht f. Neurologie und Psychiatrie.¹

The second issue of this annual review, containing the neurological literature for 1898 is in every way up to the high standard of the first issue, which we commended to our readers a year ago. The work comprises 1406 pages and 5517 titles. These are distributed as follows: Under Neurology, Anatomical Technique, 45; Anatomy, 373; Physiology, 766; Pathological Anatomy, 277; Pathology, 2571; Therapy, 574; and under Psychiatry, 885; together with 26 books not otherwise classified.

When one notices that nearly all of these titles are represented by brief abstracts, the magnitude of the work is evident. The value of the work is further increased by full author's and subject indexes, covering 98 pages. The number of typographical errors is unfortunately rather large, but this is the only criticism which we have to offer.

The publishers have prefixed a good portrait in photogravure of the editor, Dr. Mendel, in honor of the latter's sixtieth birthday, recently celebrated.

C. J. H.

¹ Jahresbericht über die Leistungen und Fortschritte auf dem Gebiete der Neurologie und Psychiatrie. Issued by DR. E. FLATAU and DR. L. JACOBSON; edited by PROF. E. MENDEL, with the coöperation of a board of 59 collaborators. Berlin, S. Karger, 1899.

LITERARY NOTICES

Physiology of Central Nervous Organs.¹

The necessity of a physiological consideration of problems in zoölogy has been forcing itself in the last five years upon the attention of students. Heretofore physiology has been in the main a study in the medical school centering about the human being or at the best dealing with other members of the vertebrate series as a means of elucidating problems in human physiology. As opposed to this a few original investigators have recently gone to the opposite extreme and have initiated the study of protozoan physiology without apparently appreciating the fact that protozoan physiology may be as special as human physiology. Notwithstanding the limited nature of this new movement, important results have already been achieved by it and, if one bears in mind that, like human physiology, it is bringing to light material for a comparative physiology and that it is not and cannot be comparative physiology, no great harm has been done by the enthusiasm of its supporters. Comparative physiology in the modern sense is essentially an unexplored region, and it is, therefore, a matter for congratulation when one who has spent much of his time in opening up this new domain, turns aside long enough to describe the general features of those parts with which he is most familiar. This has been done for the nervous system by Professor Loeb in his book entitled, *Einleitung in die vergleichende Gehirnphysiologie und vergleichende Psychologie*.

In the introductory chapter certain fundamental conceptions are considered. The physiological unit of nervous activity is the reflex. This is usually supposed to be purposeful and by some investigators maintained to involve, if not in its execution, at least in its development, some trace of intelligence and therefore to be a product of ganglion cells. But, as plants respond to light with as much reflex accuracy as animals, it is obvious that reflex action not only is not necessarily associated with ganglion cells but not even with a nervous mechanism; it may be a property of relatively undifferentiated protoplasm. The differ-

¹ *Einleitung in die vergleichende Gehirnphysiologie und vergleichende Psychologie*. Mit besonderer Berücksichtigung der wirbellosen Thiere. Von Jacques Loeb, 207 pp., Verlag von J. A. Barth, Leipzig, 1899.

ence between an animal and a plant in this respect is mainly in the greater rapidity with which an animal reacts rather than in any essential difference between its reactions and those of plants. The nervous system, then, in its simpler operations is a means for the rapid transmission of nervous impulses from sense organs to organs of reaction, muscles, etc. The question of coördinated reflexes is next considered and it is declared that coördination is mainly apparent and is brought about in any group of elements not by a coördinating center, but by that element which temporarily possesses the most rapid rate of discharge and which impresses that rate for the time being on the associated elements. If the simple and coördinated reflexes and even those aggregates of inherited reflexes that we call instincts are at bottom only delicately adjusted transmissions of nervous impulses and therefore in no sense a test of intellect, what criterion can be used for the psychic qualities of animals? To this Professor Loeb answers, associative memory. An animal to have the most rudimentary form of psychic life must have the power of associating its past nervous experience with its present. It must be able to learn. Having this power the animal may develop consciousness; without it, such a step is absolutely impossible.

Following the introduction is a series of chapters dealing in a suggestive way with the nervous activities of a graded set of animals. These include a consideration of the medusæ, ascidians, actinians, echinoderms, worms, arthropods, molluscs and vertebrates, and outline the development of nervous activities in the animal series.

The concluding chapters deal with general problems of the central nervous system, and, while these are more or less associated with the higher animals, proper treatment is accorded them, as Professor Loeb all along points out, only from the comparative standpoint. The subject matter of this part of the work includes such as the physiological aspect of the segmentation of the vertebrate central nervous organs, animal instincts, the central nervous system and inheritance, criteria for the determination of consciousness in lower animals, the brain and consciousness, and the theory of the localizations of nervous centers.

The observations recorded in this work are in the main matters with which Professor Loeb is acquainted at first hand and the vigor and accuracy of the text is doubtless owing in large measure to this fact. Here and there are questionable statements such as are to be expected in the first edition of a book covering so broad a field. Thus, in the account of the reactions of planarians, the fact that their movements are accomplished in part by muscles that are probably controlled by a nervous mechanism and in part by cilia probably independent of nervous in-

fluence is not taken into account and may have more or less to do with what is pointed out as an important difference between the reactions of Thysanozoan as a representation of marine planarians and Planaria.

From the relatively small amount of work done in this field Professor Loeb's book is of necessity only the barest framework of a structure that the future may be expected to elaborate. It has the advantage, however, of being a framework in such proportions that new workers will be more concerned with filling out its deficiencies than with tearing down its parts, and for this teachers and students alike must be grateful to Professor Loeb. The book may be said to embrace the first comprehensive rational scheme for a comparative physiology of the central nervous system.

G. H. P.

Bevan Lewis' Text-Book of Mental Diseases.¹

Few works on pathology have been more generally quoted and widely known than the first edition of this work and, while the peculiarities of the author's position have awakened much controversy, the result has been wholesomely stimulating to research.

The new edition comes to us in the familiar guise and, though augmented and partly rewritten, the changes are not such as to require a fresh estimate of the position to be assigned to the book.

Among other important changes we notice that the discussion of the nerve cell has been enriched by material relating to the contents of the cell from the recent results of Nissl, Benda, Dogiel, Bethe, Lugaro and others.

The author adopts the statement of Professor His that after the third month of foetal life the neuroblasts no longer increase in number but in size only. Although this view has been supported by the recent results of Paton² there are practical as well as theoretical considerations which make against the acceptance of the idea in its unmodified form. It is incumbent upon those who promote this theory to explain where the reserves which replace senile cells are situated.

Articles on chromatolysis, fatigue and chemical constitution of the nerve material, all in line with recent investigations, are interpolated in this chapter which also contains a discussion of the neurone theory. We are glad to notice that the term neurocyte is used for the body of the nerve cell.

¹ A Text-Book of Mental Diseases. Second edition. P. Blakiston's Sons, Phila. \$7.00.

² *Neurologisches Centralblatt*, No. 23, 1899.

The discussion of the form of the nerve cell is an interesting attempt to graft the results of the new methods upon the terminology of the original edition. The paragraph on neuroglia has been considerably modified but the spider cell of the first edition has been identified among the findings of the Golgi method. Three stages in these elements are described: (a) cells with short, thickened, moss-like protoplasmic processes, dendritic or branching dichotomously and possessing also thick vascular attachments; (b) long and exceedingly fine unbranched fibrils radiating from an obscurely marked central cell, also (under certain conditions) showing vascular processes; (c) transitional forms with vascular processes, short dendritic branches, from which are given off long delicate fibrils like those of the stellate cells, and often distinctly moniliform.

Very extensive additions and interpolations occur in the remainder of the chapter devoted to the lamination of the cortex and this portion has been enriched by numerous illustrations from silver preparations.

In the clinical chapters little change of importance is noted. A section is devoted to the description of a reaction time instrument and some tables and details have been omitted. Kleptomania, dipsomania, erotomania and obsessions are given special headings and paragraphs have been added treating of paranoia, the neuropathic basis, folie à deux, etc. Under general paralysis a figure is added illustrating the nuclei of the third nerve and also a section devoted to the significance of pupillary anomalies.

In the pathological section the author has seen no reason to change his views as to the importance of the scavenger cell. The book has retained all the peculiarities which have proven so suggestive in the first edition, while the material added has been so skilfully incorporated as not materially to impair the unity of the work. C. L. H.

Antivivisection Discussion.

The country is being flooded with literature prepared under the auspices of the American Humane Society denouncing the cruelties of scientific men. These publications boldly charge the leading scientific men of this country and especially the members of the National Academy of Science with mendacity and disgraceful artifice.

We do not propose to enter upon this discussion. Few intelligent men are duped by such statements as that no substantial gains to the healing arts have accrued from experimentation upon animals. It may be noticed, however, as a peculiar fact that the discussions put forth by this so-called humane society are singularly violent and acerbic in language and unscrupulous in the garbling of evidence so that one (like

the present writer) unfamiliar with the personnel of the writers would be driven to the belief from a simple reading of these publications, that the animus is far other than the spirit of gentleness and kindness supposed to actuate such efforts. It is our belief that no man worthy of the name will inflict what he regards as needless cruelty on animals. His appreciation of the value of the work in hand doubtless differs from that of the ignorant spectator or reader who appreciates only the details. So far as our observation is concerned, the work of vivisection is carried on in much the same spirit as that which from time to time prompts investigators to expose themselves to serious disease in order to secure subjective information of its symptoms. The propagandists the antivivisection gospel are certainly not actuated by the spirit of Him who asked "How much better is a man than a sheep?"

C. L. H.

Gowers' Manual of the Diseases of the Nervous System.¹

The first volume of this well and favorably known work is upon our table in a third edition and is presented in a substantial and attractive form. The book itself is too well known to require review and although it has been subjected to complete revision, the changes are not conspicuous.

The section which has been added on "the general constitution of the nervous system" is brief and not very satisfactory. The author seems to feel that it is foreign to the plan of the book but cannot avoid a reference to the data which, however unintelligible, are yet "changing our physiological and pathological conceptions in a manner and degree that must be adequately recognized though much of their effect is still uncertain."

From what is said it would appear that all of the recent increments of our knowledge of the anatomy of the nervous system "are the result of a method of metallic staining first devised by Golgi of Pavia." There is no hint of the important part played by methylen blue and Weigert's method, which certainly should rank as not less important means of research.

A brief statement of the neurone theory is followed by a more extended discussion of Max Schultze's theory of fibrillary structure of the nerve fiber while, curiously enough, there is not a word regarding Nissl's discoveries whose bearing here is at least fully as apparent.

In the chapter on the structure of the spinal cord by Dr. Abraham attention is given chiefly to the topography rather than the histology

¹ P. Blakiston's Sons and Co. \$4.00.

but we think some space should have been devoted to a statement of the recent results of the chrome-silver method as applied to the cord by Kölliker, Cajal and others. In passing it may be remarked that, while the make-up is generally good, we note several cases where "y Cajal" is spoken of as though "y" were a titular prefix like "von" or "de" instead of simply the word "and."

Of the pathological sections it is not necessary for us to speak here. There is no doubt that the work will long remain a standard hand-book for the use of the practitioner.

C. L. H.

Gordinier's Anatomy of the Nervous System.¹

At a time when so large a number of candidates for recognition are pressing upon our attention a new hand-book of the nervous system may expect to meet careful scrutiny. The author of the work quoted has been "convinced of the necessity for a systematic text-book which shall present this most difficult subject in a concise but comprehensive manner." In the introduction Dr. Hun indicates that the work bases its claim to recognition upon "clearness of style and profuseness of illustration."

The reader then need not expect the results of new investigations or theoretical discussions but the quintessence of what is definitely known, clearly stated and organized in such a manner as to present a consistent and intelligible view of the subject in its entirety.

It may be doubted whether any man is at the present moment in a position to accomplish this task. It is certain that no one has done it. Even the admirable book of Dr. Edinger evidently fails to present a synthetic account of the brain; in fact, one of its greatest services to science is the presentation of the limits and deficiencies of our knowledge. It is true that we have no comprehensive work adapted to be used as a student manual. Edinger's lectures are more adapted to the investigator than the medical student and we have no other up-to-date text.

So far as the second claim put forth is concerned, it is amply justified. In fullness and elegance of illustration the book leaves little to desire. The paper and topography are luxurious.

As to the book itself we confess to disappointment—a disappointment that grows as we read. It is not that there is not a wealth of material, for the author has compiled most diligently and indiscriminatingly. The old has been patched with the new with seeming disre-

¹ The Gross and Minute Anatomy of the Central Nervous System. H. C. Gordinier, M.D. P. Blakiston's Sons and Co. Price \$6.00.

gard of consequences. As a reflex of the present condition of neurology the book is realistic but as a consistent picture of the brain and nervous system it is a failure all the more regrettable for the vast amount of valuable material collected in it.

We seek in vain for the accuracy, uniformity and intelligibility that should constitute its chief claim to recognition. We are not inclined to be arbitrary in matters of nomenclature—we are heartily tired of “neuronomy”—but here, if anywhere, is a justification of the crusade for revised nomenclature. Terms of direction and position are mingled in the same sentence in inextricable confusion until, unless one knows where an organ is and whither it tends, he would be unable to discover from the description. The same thing lies in front of and ventral to some other thing which tends forward or upward or in a cephalic direction. In the description of the olives, for example, the following terms occur in the same paragraph: anterior, superior, dorsally, dorsolaterally, lateral, ventral, beneath, upward, upper, posterior, and so on to the end of the section. The terms posterior, anterior, etc., are retained in the names of parts but in descriptions the same positions are called dorsal ventral or posterior and anterior indiscriminately. The term behind is used to mean dorsal to and in the latter part of the same sentence posterior and dorsal are used in the same sense. We are treated to such novelties as “chromophyllic granules” in connection with Nissl’s discoveries, and other technical infelicities occur. These inconsistencies are perhaps less important, they are certainly less unusual, than the repeated description of the same part or organ where the several descriptions disagree in important particulars.

To cite a single instance, the “superior peduncles” are thrice described. On page 188 we read “The superior peduncles (processus ad cerebrum) appear to come from the region just beneath the corpora quadrigemina, where they decussate, extending from one cerebral hemisphere to the opposite cerebellar hemisphere.” A foot note states, however, that they run the other way. On page 229 a more extended description is given which would not be recognized as relating to the same organ, but the author adds at the close that some anatomists do not agree with what he stated. Another description is given, like the above under a full heading, on page 202 and this is materially different from the other two. While this is perhaps an extreme illustration, it indicates a fundamental and vital defect in the book.

The chapter on peripheral nerve terminations seems weak and not up to date. As a whole, it may be said that the book will prove helpful to many by reason of the collection in convenient form of so large

amount of valuable material and on account of the large series of useful illustrations but its defects are such as to tend to destroy its usefulness as a text-book for inexperienced students. C. L. H.

The Brain in Relation to Mind.

The book under the above title is by J. Sanderson Christison and is, to all appearance, privately published, as it bears no imprint. It is accompanied by a circular stating that Dr. Christison "is a specialist whose statements on the physiological aspects of the problem of the mind's relation to the brain must be received as absolutely trustworthy and that his metaphysical postulates appear to be sound and his conclusions inevitable." It is with becoming modesty then that one examines this contribution to psychology.

The earlier portion of the book is directly devoted to the destruction of materialism though on his first page he accepts with gratification J. Hughlings Jackson's assurance that the materialistic conception has been destroyed. What this metaphysical doctrine of materialism is which he now for a second time destroys our writer seems to have but a vague idea, but at any rate "it is a natural child of the current evolution idea, the greatest delusion of the 19th century." "It is not certain," we are told, "that brain cells enter into the problem at all." Somewhat inconsequently the author nevertheless devotes a large part of his book to brain and brain cells. He finds a serious draw-back to the conception that brain has anything to do with memory in the fact that memories persist in spite of the fact that the cells which are supposed to perpetuate them are many times replaced during a life time. He is quite unaware of the doctrine of neural substitution as applied to memory perpetuation and to the explanation of senile reversion to older reproductions and is guiltless of the concept of equilibrated consciousness.

Sensory impressions doubtless in some way affect brain cells but there does not seem to be any significance in this fact, there being no proof that complex thinking requires any more cells than simple mental processes and, in fact, there seems to be no reason for the existence of brain cells at all "for the brain can have a conditioning and sympathetic influence only as a *medium* of action, sensory and motor." This last statement (unintelligible to the reviewer as it must be confessed it is) settles the whole matter.

As to the main part of the book, relating (most unnecessarily for the author's purpose) to the anatomy and physiology of the brain, little need be said. It is neither full enough to be of use to the student nor

wholly devoid of mistakes in detail. The pathological data are selected *ex parte* to prove a case and are made to appear to contradict the doctrine of localization which elsewhere is admitted. The author cites the celebrated instance of the dog deprived by Goltz of its hemispheres, reported in this journal by Professor Edinger, and remarks convincingly that "he exhibited defects *only* in the manifestations of intelligence, memory, reflection and understanding." (*Italics mine.*)

We sincerely regret that we are unable to commend the book, for we believe it to have been intended to promote morality and religion ; but to accomplish such a task in the sphere selected implies familiarity with psychology and metaphysics not in evidence in the book before us. Not everyone who does not adopt the theory of psycho-physical parallelism advocated by the author is a materialist, neither does it follow because one believes in the theory of evolution that he is a materialist. It is not necessary for one who is led to admit that, as man is constituted, his mental manifestations are bound up with his cerebral activities so that both present different aspects of his personal life, to deny as a consequence the possibility of mental manifestations elsewhere and otherhow. Truth is after all the greatest thing that man can seek and a willingness to recognize it wherever it appears is not so dangerous as our author appears to feel.

C. L. H.

The Nervous System, by Lewellys F. Barker.¹

The revolutions in our knowledge of the structure of the nervous system occasioned by the phenomenal activity within the last decade of students of the newer methods of research naturally involves the necessity on the part of the text-book writers of a readjustment to the new points of view. The recent editions of the standard works all illustrate this effort for readjustment, and in most cases, it must be confessed, with only indifferent success. But here we have a new work with no precedents behind it, elaborated for the sole purpose of presenting the new neurology in systematic order. It is, of course, a truism that the key to nervous structure is function, and the text-book of the future will include not only a detailed exposition of the course of the fibers from the cell-bodies of every functionally distinct nucleus but also all of the functional connections of whatever sort possessed by these cells. It is needless to add that Dr. Barker's work falls far short of such an ideal. The

¹The Nervous System and its Constituent Neurones, by Lewellys F. Barker. Designed for the Use of Practitioners of Medicine and of Students of Medicine and Psychology, with two colored plates and 676 illustrations in the text, pp. xxxii-1122. New York, D. Appleton & Co., 1899.

time is not yet ripe for it, as our fund of knowledge is still far too meager. But this work does give a very faithful picture of the status at the present moment; and it is much more than this, for Dr. Barker has done what some of our pioneers in the newer fields have signally failed to do—he has correlated these newer findings with the classical works by the older methods. Herein perhaps lies the chief value of the work, for the bibliographic labor expended has been enormous and the facts are presented in such a way as to be really accessible to the reader so far as they go without consulting the original papers. This is largely due to the surpassing richness and excellence of the illustrations.

As a work of reference, therefore, it is invaluable, since it gives quite complete pictures of the whole of our knowledge regarding every detail of the structure touched upon. The book falls into six sections, as follows: (1) The History of the Development of the Neurone Concept, (2) The External Morphology of Neurones, (3) The Internal Morphology of Neurones, (4) The Histogenetic Relations of the Neurones, (5) The Neurone as the Unit in Physiological and Pathological Processes, (6) On the Grouping and Chaining together of Neurones in a Complex Nervous System like that of Man and Higher Animals. The last section includes more than two thirds of the entire work. The fourth section is undoubtedly the weakest, the materials not being chosen from as wide a field as might be desired, nor are those selected very well organized. As illustrating the difficulties in the classification of the matter, one notices that, though a chapter in Section 4 is devoted to the segmentation of the body, yet the most important data on this subject are to be found in two other places, in connection with the sensory and motor nerves in Section 6. It would seem better to have brought these together, even at the expense of logical analysis.

The work is not well adapted for an elementary text-book, the material presented being too voluminous and much of it too technical; it was doubtless not so intended, as evidenced by the absence of any systematic presentation of the general gross topography. As a reference book there are a few points in which improvements might be suggested. For example, the bibliographical citations would be of much more value for easy consultation if they were gathered together at the close of the work instead of scattered in foot notes. This too would have saved some repetition—an important item in a book as large as this. The latter point applies also to the figures, some of which are repeated many times, when a simple cross reference would have answered as well and materially decreased the number of pages. The

book is provided with author's and subject indexes, but neither of these is as complete or free from error as should be the case in a work of this character. It is not to be expected that the literature of all parts of so vast a field should be worked over with equal care. In some cases, as in the account of the peripheral gustatory neurones, the presentation gives a false (or at best a very incomplete) view of the present status. Questions of nerve components are briefly touched upon under the head of the peripheral motor neurones. One would have expected this principle to have received recognition also in the classification of sensory impressions, where it is of still more importance to sound morphology, but here we see no use made of the idea of functional systems as introduced by Strong. Finally, we feel inclined to deprecate the appearance of special pleading for a particular phase of the neurone theory, notably evident in the discussions of the anatomical independence of the nerve units, and manifested especially in a tendency to minimize the importance of conflicting evidence.

Taken as a whole the work is a remarkably able and objective summary of present knowledge. Dr. Barker possesses the rare gift of being able to give in few words a useful and readable abstract of an intricate discussion, and he has put all working neurologists under very special obligations in the present contribution. The reviewer has read every one of his pages, and all with interest, as well as profit.

C. J. H.

Bibliographica Medica.

The *Index Medicus*, after having been carried at a financial loss for many years by the American publishers, was suspended last year for want of support. Following its demise, there appears from Paris, beginning with January of this year a monthly bibliography planned along similar lines and designed to succeed the *Index*, as a universal bibliography of the medical sciences. It is published by the "Institut de Bibliographie," edited by Marcel Baudoin, under the direction of C. Potain and Charles Richet. The price is (to foreign countries) 60 Fr. per year.

C. J. H.

Le Nevrxax.

Under the title "*Le Nevrxax, Recueil de Neurologie Normale et Pathologique*," a new journal is issued from Louvain by Professor van Gehuchten. For several years neurologists have welcomed the semi-annual "*Travaux*" from his laboratory, made up chiefly of the reprints from various journals of his own work and that of his pupils. The motive for the new journal lies in the need for greater promptness and

uniformity in the publication of these results; accordingly it continues the *Travaux* along similar lines, though outside contributions are solicited also. Three numbers make a volume, the fascicles to appear at irregular intervals. We extend to our colleague hearty congratulations upon the amount and quality of the researches which have been issued from his laboratory since the first appearance of the *Travaux* in 1897.

C. J. H.

Gould's Medical Dictionaries.¹

The publishers announce that 100,000 of these dictionaries have been sold. New editions of the three popular issues are announced, the latest being the pocket size. This compact and richly bound little book ($1 \times 3\frac{1}{2} \times 6$ inches) contains 837 pages, definitions and pronunciations of 30,000 words, with numerous useful tables, and sells for \$1. It cannot take the place of the author's larger dictionaries, as the definitions are too brief; they are however adequate in most cases to their purpose and the list is very complete and well chosen. C. J. H.

Information Wanted.—The psychophysiology of anæsthesia is a productive subject greatly in need of adequate investigation and discussion. Both pure science and practical surgery have doubtless much to gain from a deeper-going study of experiences under ether, chloform, nitrous oxide, etc., than has as yet been made. Scientific literature has frequently contained accounts of isolated individual experiences reported most often because of their strangeness. A very large number of descriptions of the ordinary experiences is what is now desired, and to this end blanks have been prepared on which replies to certain simple questions may be written. All persons, and especially hospital surgeons, officers of medical societies, and instructors in medical schools, are respectfully requested to send to the undersigned for as many blanks as they care to distribute among persons who have been under an anæsthetic. These will be gratefully sent, and received when filled out. GEORGE V. N. DEARBORN.

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¹ Published by P. Blakiston's Son & Co., Philadelphia.

LITERARY NOTICES.

Van Gehuchten's *Anatomie du Systeme Nerveux*.¹

Professor Van Gehuchten's Text-book has passed through three editions at intervals of three years, the present edition being nearly twice as large as the first. The arrangement is, however, the same, comprising an exhaustive treatment of both the central and the peripheral nervous systems. The work falls into two great divisions, The Cerebro-spinal Nervous System, and the Sympathetic Nervous System, the latter comprising 24 pages out of a total of 1052. The lectures on the cerebro-spinal system are grouped under three general heads, (1) The Gross Anatomy of the Axis Cerebro-spinalis, (2) The Internal Structure of the Axis Cerebro-spinalis, (3) The General Structure of the Cerebro-spinal System, the latter being a résumé in seven chapters designed to give "the quintessence of all that students of medicine and physicians ought to know of the structure of the nerve centers." Under the second head there are six lectures devoted to General Considerations upon the Nervous Elements, followed by the discussion of the several regions of the central system, the peripheral nerves being presented in connection with their centers.

Professor Van Gehuchten has himself had a large part in the shaping of neurological opinion during the past decade and we naturally turn with interest to his General Considerations, as expressing his latest opinions upon a number of debatable questions. In this work he reaffirms his earlier views of the independence of the neurones and treats all undoubted cases of anastomosis as wholly exceptional, freaks or monstrosities. In the reviewer's opinion this extreme position is hardly supported by the facts now at command. Unquestionable cases of anastomosis are too numerous and too important to be dismissed in this way, though this of course does not imply any theory as to what their significance really is. The author states the opposing views of Apathy, Held, Bethe and Nissl very fully, but it would appear as if he gave them hardly sufficient weight. He does well, however, to insist that the most important of the conclusions of these articles are highly the-

¹ *Anatomie du Système Nerveux de l'homme: Leçons professées à l'Université de Louvain.* 3d. edition, 2 vols. Louvain, 1900.

oretical and to urge that we suspend our judgment until more proof is furnished. He also mentions a point which many of these critics seem wholly to overlook; viz., that the question of anastomosis or complete anatomical independence of nerve cells is only one aspect, and that too a relatively unimportant one, of the general doctrine of the neurone. The real issue is, Can the cell theory be applied in the nervous system and is the nerve cell in its entirety (neurocyte or neurone) a unit of value in the simplification of our morphological, physiological and pathological data? The experience of the last decade leaves no doubt on this point and we have every reason to look forward to a great extension during the decade now opening of the usefulness of this point of view. Certainly this conception is not incompatible, as several recent authors have pointed out, with intercellular anastomoses of the most diverse and extensive sort, such as we recognize in other tissue systems without feeling obliged to throw over the cell theory.

Professor Van Gehuchten adheres to his original theory of the polarization of the neurone and defends it at some length against recent objections. He admits the experimental proof of Sherrington and others for double conduction in the central nervous system, but believes that this experimental condition is not realized in the normal physiological functioning.

The facts bearing upon the theory of amoeboid movements of nerve cells are passed in review. The author believes that it has been proven that in certain experimental conditions the filiform appendages or thorns of the dendrites of cortical nerve cells may be shortened (during cellular activity), or even abolished with varicosity of the dendrites (extreme fatigue and certain intoxications). But whether this involves active amoeboidism of the cells as a normal physiological process, disturbances of their nutrition or some other factor cannot be decided in the present state of our knowledge. As to the significance of the chromatic or tigroid substance in the nerve cells, he regards it as established that it accumulates in the cell during repose and diminishes during activity. Any disturbance of the normal relations of the cell may result in its loss. It therefore represents reserve material, not a substance indispensable to the nervous elements.

On some of these debatable questions, and others which might be mentioned, the author's position will be regarded by many neurologists as rather too radical. His statements are, however, usually made with due caution or reserve, and in particular, the evidence for contrary opinions is fully presented. Dogmatism, even in a text-book, on these subjects would be out of place and the author has doubtless chosen

the wiser course in stating his own views clearly with the evidence for and against. The work is thoroughly brought up to date and gives a very good picture of the present state of the subject in most of the sections. The mechanical features of the book leave much to be desired. All neurologists are familiar with the many ingenious and clear diagrams with which the author's works abound. Many of those in these volumes were drawn after the figures which he is in the habit of drawing on the blackboard for his students during his lectures. Too often, it must be admitted, they still exhibit the crudities of the blackboard sketch. For many of the subjects, especially those concerned with cytological details, a larger number of carefully finished drawings would add greatly to the value of the work.

C. J. H.

Whitehead's Anatomy of the Brain.¹

The first impression one gets from this booklet is pleasing. There is a field for a short and concise exposé of the nervous system, and at first sight the book seems to furnish the necessary number of drawings for the illustration of the principal data.

On careful reading and study of the drawings, the judgment cannot be as favorable. We have the impression that little is done in these pages which could not with advantage be compressed into a much better tabulated glossary of the illustrations with concise definitions of the terms and reference to all the illustrations in which a certain part appears.

The method of description is mainly topographical. We can imagine the text to be the talk accompanying a concise demonstration, but we miss the pointing of the fingers, the chance to see the whole specimen, etc., which as a rule is taken in much more promptly than the stream of words of a lecture and leads to an undercurrent of broader attention in the student than the talk alone would arouse. In a book, the "talk" is not at its best in topographical description, unless there be a well-tabulated guide to the study of illustrations, and the text be a genetic description of the parts under study with the suppression of all unnecessary topographical description which the student will grasp better from a set of illustrations or sections or models. For such a genetic study it would, however, hardly do to omit the description of cord and peripheral nerves.

¹ The Anatomy of the Brain. A Text-book for Medical Students. By RICHARD H. WHITEHEAD, M.D., Professor of Anatomy in the University of North Carolina. Illustrated with Forty-one Engravings. $6\frac{1}{4} \times 9\frac{1}{2}$ inches. Pages, v-96. Extra Vellum Cloth, \$1.00, net. THE F. A. DAVIS CO., PUBLISHERS, 1914-16 CHERRY ST., PHILADELPHIA, PA.

Considering the fact that it is by no means clear what a medical student wants from a study of the brain—usually he cares for little more than a vocabulary to cover up his ignorance—it is difficult to say what plan had best be followed by a book. Without a study of brains in the laboratory little of real value is to be gained. But for a guide in laboratory work the book is not arranged systematically enough, and for reading without laboratory facilities, it has not enough illustrations, nor does the text try to keep in the limits of that which the illustrations can show.

We regret to make this adverse criticism and should probably have judged otherwise without a rather careful reading of the text and figures, and if we had not frequently tried ourselves to find the best way of presentation of this rather difficult topic. In illustration of our criticism, we refer briefly to the disadvantages coming from dividing the brain into five or more vesicles, which leads to an utterly inadequate description of the forebrain and to such statements as: "In the embryo the isthmus exists as a separate *vesicle*" (p. 15), the confusing description of the hindbrain and, for instance, of the lateral recesses of the fourth ventricle. I also mention the statement (p. 20) that the corpus geniculum laterale is said to be connected with the anterior arm of the mesencephalon (brachium quadrigeminum superius). In Fig. 12 the s. occipitalis transversus of Van Gehuchten's drawing is called parieto-occipital fissure; the central fissure does not cut into the edge of the longitudinal fissure; Fig. 15 could easily be replaced by a clearer and more correct one, and Fig. 9 is probably also too difficult to grasp without several other drawings. The sections of the brain stem are over-schematic, and the description fragmentary. The use of the words "anterior," etc. (e. g., anterior olive) is often confusing.

We wish to say though, that many parts might well take the place of lecture notes and that on the whole the description of the sections is more easily followed than the macroscopic description and the data which require reconstruction. The writer shows that he knows the recent literature, and especially his van Gehuchten, quite well and he embodies many points which might appear unessential for the student and certainly not easily intelligible without the free use of drawings.

The experience in the class-room will show to what extent the book will find friends. Its small size will certainly do much to make it attractive to the beginner.

A. M.

Les Actualites Medicales.¹

In a booklet of 95 closely printed pages, the well-known clinician of Montpellier puts together the anatomical data which are of importance for the student of nervous diseases. In the first (general) part (p. 1-12) he gives a summary of the "neurone," the connection of the neurones, their grouping into systems, and finally, a sketch of the growth of these systems. In the second part he deals with motility and general sensibility, vision, hearing, taste and smell, language and circulation, respiration and digestion.

The presentation is somewhat dogmatic, as is necessary for the didactic purposes of the little work, but concise and clear. There are numerous references to literature, most of which are very well chosen, many from French and German sources, but perhaps all the more instructive for us. Only 11 figures and 4 summarizing tables accompany the text, and it is obvious that the author does not want to do more than to arrange from the point of view of the clinician some of the material which the anatomists arrange from the point of view of morphology.

A. M.

Mentally Deficient Children.²

The well known little compend has grown from 140 to 180 pages. Apart from some changes in the old chapters, there are two new ones, "giving some account of the inquiry undertaken for the Education Department by the committee of which the author had the honor to be a member,—and also of the practical measures adopted for special instruction by several school authorities, and notably by the School Board of London."

The book deals in a very concise manner mainly with the practical questions connected with this problem and furnishes relatively little for the student of neurology. But it deserves the attention of everybody who has any interest in the broadening out of pedagogy and the cooperation between pedagogical and medical measures, and, therefore, deserves high recommendation.

A. M.

Hoffmann's Contributions to Selachian Embryology.

Among the more extensive of the recent contributions to Selachian Embryology is C. K. Hoffmann's "Beiträge zur Entwicklungsgeschichte der Selachii" in Gegenbaur's *Morphologisches Jahrbuch*. The

¹ Anatomie clinique des Centres Nerveux par le Dr. Grasset. Paris, Librairie I. B. Baillière et Fils. 1900.

² Mentally Deficient Children: Their Treatment and Training. By G. E. Shuttlesworth, B.A., M.D., etc. Second edition. London, H. K. Lewis and Philadelphia, P. Blakiston's Son & Co. 1900.

first of these contributions appeared in Vol. XXIV, 1896, and included the following parts: I, Gastrulation; II, the Anlage of the middle Germ Layer and Chorda; III, The Anterior Head Somites; IV, Olfactory Organ; V, Mouth and Hypophysis. The second article, in Vol. XXV, 1897, includes: VI, the 4th and 5th palingenetic Head Somites; VII, the 6th palingenetic and the 4 cenogetic or occipital Somites; VIII, Ventral Nerve Roots of the Head Somites; IX, Development of the IV Nerve. The third article appeared in Vol. XXVII and contains part X, Development of the Dorsal Nerve Roots of the Head Somites.

Hoffmann supports the general view that both sensory and motor roots of the nerves of the branchial type correspond to dorsal roots, these segments lacking ventral roots. All post-vagal motor roots, however, represent ventral roots of nerves of the spinal type, and the same is true of the VI and III nerves; but the IV nerve he regards as a dorsal nerve. It belongs with the same segment as a portion of the trigeminus. In fact, the trochlearis and the portio trigemini rami ophthalmici superficialis are one and the same nerve. They separate only in late embryonic stages and there is always a fibrous connection between them in the adult, as Schwalbe has described.

The branchiomeric nerve is regarded as a dorsal nerve. Its typical composition in selachians includes a dorsal ramus and a ventral ramus. The latter gives off (1) the r. post-trematicus, of mixed sensory and motor function and regarded as the continuation of the trunk of the nerve; (2) the r. pre-trematicus, wholly sensory; (3) the r. pharyngeus, wholly sensory.

The trigeminus and facialis are both regarded as double, or dimetameric, nerves, the former divisible into the "thalamo-ophthalmicus" and the "trochleo-trigeminus," and the latter into the "ophthalmico-buccalis" and the "acustico-hyoideo-mandibularis." The author's scheme of the primitive metamerism of Acanthias is somewhat as follows: The ventral nerve of the first somite (excluding the anterior head cavity of Miss Platt) is the oculomotorius, its dorsal nerve the "thalamo-ophthalmicus," or profundus, or thalamicus nerve. In early stages its ganglion is distinct, viz., the g. ciliare of Van Wijhe, the g. mesocephali of Beard. Hoffmann calls it the g. ophthalmici. It fuses with the skin and third nerve, then separates from the skin and withdraws from the oculomotorius, but retains fibrous connection with the latter, and grows toward the trigeminus ganglion (of the next following segment), finally fusing with it. A ciliary ganglion belonging to sympathetic system appears more distally on the third nerve and con-

nected with the thalamic ganglion by a fibrous strand. From the brain to the thalamic ganglion Hoffmann calls this nerve the "thalamic," from the ganglion distally, the "ophthalmicus profundus."

The ventral nerve for the second somite is lost, the dorsal nerve being the "trochleo-trigeminus." This nerve gives rise to the trochlearis and all of the trigeminus except the r. ophthalmicus profundus. Its gill slit and gill bar are lost. Its ganglion is termed the g. trigemini, and the term g. Gasseri is applied to the fused product of the union of the g. trigemini and the g. ophthalmici. The abducens is the ventral nerve of the third somite, its dorsal nerve is the "ophthalmico-buccalis," viz., the r. ophthalmicus superficialis facialis and the r. buccalis. The ophthalmic represents the dorsal branch and the buccal the post-trematic ramus of the ventral branch, primitively running out on the mandible.

The fourth and fifth somites have no ventral nerves. The dorsal nerve of the fourth is the "acustico-hyoideo-mandibularis," the acusticus representing the dorsal branch and the hyoideo-mandibularis the post-trematic ramus of the ventral branch. The palatine and pre-trematic branches run down in the typical way in front of the spiracle, this being the first segment to exhibit all of the typical branches of a branchial nerve. The fifth somite is in the same way related to the glossopharyngeus, this nerve forking around the first true gill cleft in the typical way.

As a matter of fact the relations in the adult do not accord with this scheme, for the trigeminus does not form the ventral branch of a branchial nerve in front of the mandible, nor does the buccalis form the ventral branch of the segment containing the mandible. The author, not finding any evidence of the suppression of a branchiomere between the mandible and the hyoid, therefore assumes that there has been a degeneration of gill arches and clefts progressing caudad and that the ventral ramus of the trigeminus thus came to lie in the mandible as a secondary arrangement. The proper nerve of the mandible was then crowded out of its own segment and suffered change of function to supply the infra-orbital lateral line canal.

This argument seems to the reviewer forced and unnatural. But the original and primary metameric scheme upon which the argument is based exhibits a much more fundamental defect; viz., the old error of homologizing disparate structures. The dorsal branches, for instance, of his pre-otic nerves are in some cases general cutaneous and in other cases lateralis nerves. It may be regarded as thoroughly established that the whole lateral line system is cenogenetic and possesses abso-

lutely no metameric value of its own. Its nerves cannot be used as criteria to metamerism, at least not directly, as general cutaneous nerves may. This applies to the author's discussion of the post-otic branchial nerves as well. The use of the peripheral nervous system as a criterion of metamerism is always attended with difficulty and it is absolutely worthless in this connection unless the qualitative differences in the nerves themselves are taken into consideration. C. J. H.

Miss Sabin's Model of the Medulla Oblongata.¹

Although the preparation of Miss Sabin's models has brought out comparatively few facts which are actually new to science, nevertheless it must be regarded as a notable feature of current neurological progress. This is the first time that the spatial relations of the internal organs of the medulla oblongata and adjacent parts have been presented in three dimensions with anything like completeness. The descriptions and figures which Miss Sabin gives of her models are of great value to all teachers and students of morphology. We should like to see reproductions of the models themselves put upon the market.

C. J. H.

Schaper on the Elements of the Selachian Retina.²

The facts which Dr. Schaper brings out in this beautifully illustrated little paper are interesting chiefly because they picture the elements of the retina as seen in surface preparations made with methylene blue intra vitam and thus permit a comparison of the results of this method with the study of the same subjects by Golgi's method made by Retzius and Neumayer. His results, as was to have been expected, while not contradicting theirs, nevertheless supplement them in many particulars and add to our knowledge of the inter-relations of these elements. No neurites were discovered for the amakrine cells of the inner granular layer, but the so-called bipolar cells of that layer have short axis cylinder processes all directed *centripetally* and apparently terminating in the inner plexiform layer. Anastomoses were not observed between any of the retinal elements. This work emphasizes again the necessity for abundant control of both the Golgi and methylene blue methods. Successful methylene blue preparations in general seem to give a more complete impregnation of the ultimate termini of the cell processes than the Golgi method can furnish, though probably requiring more skill and experience for their true interpretation.

C. J. H.

¹ A Model of the Medulla Oblongata, Pons and Midbrain of a New-born Babe. By FLORENCE R. SABIN. In Contributions to the Science of Medicine, dedicated by his Pupils to William Henry Welch on the 25th Anniversary of his Doctorate. Johns Hopkins Press, Baltimore, 1900, pp. 925-1046, with 8, plates and 52 text-figures.

² Die nervösen Elemente der Selachier-Retina in Methylenblaupräparaten, by DR. ALFRED SCHAPER. *Festschr. für v. Kupffer, Jena*, 1899.



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